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Full Name of Author — Nom complet de l'auteur
Kenneth Wayne Bishoff

Date of Birth — Date de naissance
16 September 1942

Country of Birth — Lieu de naissance
Canada

Permanent Address — Résidence fixe
c/o 4027 Dovercroft Rd. S.E.
Calgary, Alberta
T2B 1Z6

Title of Thesis — Titre de la thèse
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Name of Supervisor — Nom du directeur de thèse
Dr. Arthur W. Bailey

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YIELD, USE AND CHEMICAL COMPOSITION OF FORAGE IN ELK ISLAND NATIONAL PARK, ALBERTA

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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PERMANENT ADDRESS:

c/o 4027 Dovercroft Rd. S.E.
Calgary, Alberta
T2B 1Z6

DATED September 23, 1981

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled YIELD, USE AND CHEMICAL COMPOSITION OF FORAGE IN ELK ISLAND NATIONAL PARK, ALBERTA submitted by KENNETH WAYNE BISHOFF in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in RANGE MANAGEMENT.

Arthur W. Bailey

Supervisor

Edward S. Telfer

E. Ann Clark

Date May 25, 1981

Abstract

A study was conducted during 1977 and 1978 in Elk Island National Park, Alberta to assess the habitat and forage resources within an enclosed, 723 ha area that was heavily stocked with moose and elk. The objectives of the study were to classify and describe the vegetation, to determine forage yield and chemical composition and to describe resource utilization.

The vegetation was classified physiognomically, and by ordination and cluster analysis. The four communities described were forest, upland grassland, shrub fen and grass-sedge fen. The yield of current annual growth and use of woody browse in the forest community averaged 8 and 18 kg/ha, respectively. Similar figures for the shrub fen community were 65 and 140 kg/ha. *Corylus cornuta* and *Salix* spp. contributed most to browse yield.

Annual yield and use of forage after summer grazing in the grassland community were 3255 and 1010 kg/ha, respectively. Similar figures for two phases of the grassland community were 3211 and 1304 kg/ha for the grassy phase, and 3299 and 715 for the shrubby phase, respectively.

Herbaceous forage in the grass-sedge fen community was comprised of a sedge component and a marsh reed grass component. Annual yield of *Carex* spp. was 3721 kg/ha in 1977 and 4316 kg/ha in 1978. Similarly, yield of *Calamagrostis canadensis* was 3067 and 4124 kg/ha, respectively.

Significant differences were observed among forage classes and among species for each chemical constituent. Phosphorus, ash, acid-detergent fibre and acid-detergent lignin declined significantly from summer to winter. Generally, annual herbaceous forage and current annual growth of browse provided nutrients adequate for maintenence, but two and three-year-old wood was probably nutritionally deficient.

All habitats were utilized extensively except the grass-sedge fen. Forage preference and avoidance of 10 browse species was not attributed to chemical composition, but was attributed to several other factors, particularly forage availability. Hypothetical estimates of daily forage intake indicated that carrying capacity was exceeded during 1977, but was closer to acceptable levels during 1978.

Decreased stocking rate, prescribed burning, clearing and periodic monitoring of forage, are ways suggested to ensure sustained productivity of range and wildlife.

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I. Introduction

The survival and productivity of wildlife ultimately depends upon habitat which provides the basic requirements of food, water and shelter. Diverse habitat enhances wildlife survival and productivity by enabling animals to exercise control over various options related to feeding, social and other behaviors. Successional stage of vegetation is an important factor related to habitat diversity. The structure of vegetation based on succession permits an animal to select cover that is best suited to its need at any given time. Since each cover type has its own characteristic floral composition, alternate sources of forage are made available. This permits a choice of forage; a choice which is often influenced by palatability and/or season. Habitat diversity is also the result of topographic features of the landscape such as slope, aspect and elevation. Such physiographic features, which offer protection from inclement weather and enemies, are additional ways in which habitat diversity influences the survival and productivity of wildlife.

Another important factor affecting wildlife survival and productivity is the relationship between forage quantity and forage quality. Studies with domestic ruminants have shown that for diets of low digestibility (i.e. quality), there exists a positive correlation between voluntary dry matter intake and digestibility (Maynard and Loosli 1969). The reverse is true for diets which are highly digestible

(Blaxter et al. 1961; Conrad et al. 1964). Ammann et al. (1973) found a similar relationship between dry matter and energy intake in relation to digestibility for white-tailed deer (*Odocoileus virginiana*)[1]. When fed diets of medium to high digestibility these deer were able to maintain a constant energy balance, near maintenance requirements, by adjusting dry matter intake. For diets of low digestibility, energy intake decreased with a decrease in dry matter intake. The physical limitation of the rumen to expand, plus the slow rate of passage of low quality forage through the digestive tract, restrict the amount of nutrients that are made available for metabolization. Thus, even though a plentiful supply of forage is available, if it is of low quality animal productivity and even survival may be in jeopardy. An assessment of the habitat and forage resource therefore, is essential to the proper management of rangeland for the production of wildlife.

As an integral part of wildlife habitat, forage is a major factor affecting wildlife survival and productivity. Elton in Van Dersal (1938) stated, "the primary driving force of all animals is the necessity of finding the right kind of food and enough of it." Thus, two critical aspects of forage are quantity and quality.

An amount of good quality forage sufficient to sustain animals is usually available on native rangeland throughout most of the growing season. However in northern environments of North America, much of this forage becomes unavailable to grazing animals in winter due to snow cover. Availablility of forage on winter range is a critical limitation affecting wildlife populations. Accordingly, calculation of carrying capacity of wildlife range is based upon the supply of available winter forage which necessitates the quantification of forage yield and subsequent use. Various studies have centred on such quantification to determine carrying capacity in Elk Island National Park (EINP) (Van Camp and Telfer 1974; Telfer 1976).

---

[1] Scientific names of mammals follow Banfield (1974).

Another aspect of forage is quality. One index of forage quality is the concentration of chemical constituents relative to the nutritional requirements of the grazing animal during various seasons (Cook 1972). Deer populations in North America have shown direct responses to qualitative aspects of their food supply (French et al. 1956; Klein 1970). These studies point out the relevance of determining the nutrient composition of forage.

In addition to being a means of sustenance, forage quantity and quality influence the preference and selection of habitat and forage by animals (Heady 1964; Stoddart et al. 1975). Bison (*Bison bison*) prefer grass and sedge over other classes of forage which restricts them to use of grasslands and sedge meadows (Telfer and Cairns 1979;

Reynolds et al. 1978). Moose (*Alces alces*) prefer browse[2] compared to other types of forage, particularly in early successional habitats (Peterson 1955; Peek 1974). Telfer (1978) reported moose utilization was positively correlated to browse production in three areas of Alberta. Penner (1978) found that moose in the Northwest Territories preferred certain willow plants and species whose morphology had been influenced by previous browsing. Wapiti (*Cervus elaphus*) are mixed feeders showing considerable flexibility in diets (Knight 1970).

The forage resource of the Mixedwood Region of the Boreal Forest (Rowe 1972) is particularly suited to supporting a mixed population of native grazing ungulates because of its diverse habitat and species (Telfer and Scotter 1975). In this forest region a research program was initiated at the University of Alberta to investigate factors related to wildlife productivity (Hudson 1980). As part of this program, two research projects were begun during the winter of 1977 in a portion of the Isolation Area of EINP. One was an animal behavior study conducted to investigate habitat utilization and resource partitioning by a mixed population of elk and moose. The second was a forage resources study conducted by the author to evaluate the forage resource. The specific objectives were:

---

[2] Woody forage consisting of twigs and/or leaves.

1. to classify and describe the vegetational mosaic.

2. to determine the yield and use of forage.

3. to determine the chemical composition of forage classes and of some important forage species.

4. to discuss resource utilization relative to habitat and forage preference, and carrying capacity.

II. The Study Area

A. Size and Location

Elk Island National Park lies in the northern part of the Beaver Hills in central Alberta, 37 km east of the City of Edmonton (Figure 1). The Park is approximately 22.5 km from north to south and 10 km from east to west, centred on a point 53° 37′ north latitude and 112° 58′ west longitude. The study area was the 7.23 km² Canadian Wildlife Service compound, located in the southwest corner of the Isolation Area, and includes sections 31, 32 and the northeast and northwest quarters of each of sections 29 and 30 of Twp- 52 R-20, west of the 4th meridian. A 2.1 m pagewire fence separates the study area from the rest of the Isolation Area.

B. History and Development

The Beaver Hills offered a rich hunting and trapping ground to the Indian tribes which roamed them before the arrival of the first white explorer to Alberta, Anthony Henday, in 1756 (Griffiths 1979). Soon after, other explorers arrived and tapped this plentiful resource. A prosperous fur trade soon emerged. However by 1870, excessive hunting and trapping had so decimated beaver (*Castor canadensis*) and bison populations that many Indian bands were forced to leave the area in search of new frontiers (Griffiths op cit.).

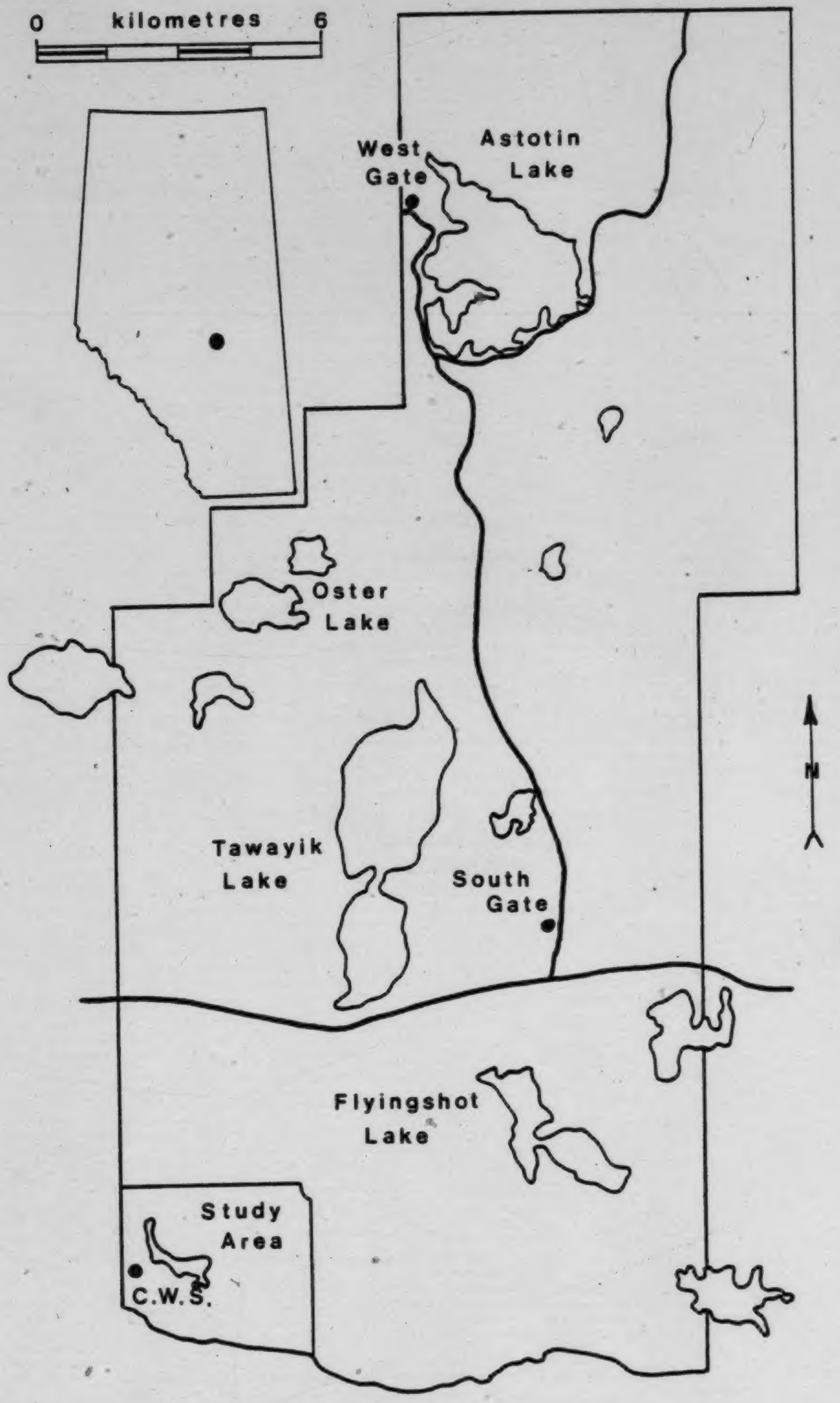

Figure 1. Map of Elk Island National Park and the location of the study area.

The 1890's marked the beginning of homesteading (Griffiths op cit). Land clearing operations, especially the repeated use of fire, effectively removed bush and along with it, prime wildlife habitat. Land clearing, together with previous heavy hunting and trapping, resulted in a scarcity of many wildlife species by the end of the 1800's (Griffiths op cit.). A few concerned citizens petitioned the federal government to take action.

In 1906, a 41 km² game preserve was erected for the protection of one of the few remaining elk herds in Alberta. Soon after completion, it was used as a temporary holding area for 410 plains bison, part of 716 enroute from Montana to the unfinished Buffalo National Park near Wainwright. During the subsequent round-up of the bison in 1909, 48 bison escaped capture, eventually becoming the forerunners of the present herd.

The reserve was officially declared a Dominion Park in 1913 (Griffiths op cit). It was enlarged by 93 km² in 1922 to accomodate the growing ungulate population. By 1930, it had gained national park status and was named Elk Island National Park. At that point The Park consisted of the area presently north of Highway 16, and is referred to as the "main park". A further 62 km² of land, previously part of the Blackfoot Grazing Lease, was obtained for expansion in 1947. This acquisition, referred to as the Isolation Area, has held a small herd of wood bison since 1965. The Canadian Wildlife Service compound with its laboratory facility and corrals, has served as a base of operation for the control and eradication of brucellosis and tuberculosis from the wood bison herd.

C. Management

Due to the lack of natural predators and probably the presence of the game fence, ungulate populations grew unchecked, thereby placing a heavy burden on the forage resource. Since 1927, periodic slaughters and selective hunts by Parks Canada personnel have maintained proper stocking rates. More recently, plains bison have been relocated to parts of Alberta and elsewhere, and some small breeding herds have been sold at auction, to ease the burden on the forage resource. Hay grown for winter feed in the Farm Area of the Park (north of Highway 16) also helps to offset feed shortages. Fences have been erected to control and facilitate animal distribution and handling, and to accomodate public observation.

The main park has also been managed for recreational pursuits. Astotin Lake has facilities for swimming and boating; other uses include golfing, camping and nature trails with guided walks in season. Numerous trails exist for cross-country skiing. Although the Isolation Area has remained closed to the public, it is scheduled to be developed for public recreation in the 1980's.

D. Climate

The climate is described as cool continental, sub-arid to sub-humid, with cold winters and warm summers (Bowser et al. 1962; Wonders 1969). Temperatures range from about -40 to +32 degrees celsius. The frost-free period ranges from 50 to 150 days and averages 100 days. Average annual precipitation is 400 to 450 mm; 70% falls as rain during May, June and July (Table 1). About 125 cm of snow falls annually. Average wind velocity is less than 26 kph and is generally from the northwest. The sun shines an average of 2,175 hours per year (45% of possible), 60% of this during the growing season (Wonders 1969).

E. Geology and Topography

Bedrock of the Alberta Plains physiographic region consists of relatively horizontal, sedimentary strata of variable age overlain by glacial drift and underlain by Precambrian rock (Lang 1974). EINP is underlain by the Edmonton Formation which consists of upper cretaceous bedrock formed in freshwater from shales, sandstones, clays and coal interbeds (Bayrock 1972). The older Bearpaw Formation, formed in a marine environment from shales, siltstones and microfossils, also underlies a small part of the Park.

These and other strata were periodically overrun and eroded by massive ice sheets. The most recent ice sheet was the Laurentide during the Pleistocene epoch about 11,000

Table 1. Total annual precipitation (mm) and snowfall (cm) recorded at Fort Saskatchewan, Alberta - Environment Canada meteorological station.

Month	Total Precipitation		Snowfall	
	1977	1978	1977	1978
January	24.8	13.6	24.8	13.6
February	T	7.8	0	7.8
March	18.7	11.0	14.9	1.8
April	17.0	18.3	3.3	0
May	125.3	76.5	T	0
June	19.9	51.7	0	0
July	88.2	110.3	0	0
August	82.5	77.3	0	0
September	39.4	120.9	0	0
October	0.5	10.3	0	0
November	7.4	29.3	7.4	16.3
December	19.1	30.2	19.1	30.2
Total	441.7	557.2	69.5	69.7

years B.P. (Bowser et al. 1962). Following the retreat and melting of ice during the late Wisconsin period, there remained glacial debris in the form of ground and hummocky moraine. The Park is situated in the Cooking Lake moraine which rises 30 to 60 m above the surrounding plain. Elevations range from 710 to 760 m above sea level.

Topography is generally knob and kettle characterized by a series of low hills and depressions, but more gently rolling and flat terrain also exists (Lang 1974). Two large lakes and several smaller lakes, sloughs and beaver ponds are within the study area. The largest water body is Walter Lake. Most streams and creeks are intermittent and carry water only during spring.

F. Soils

Soils are mainly those classed in the Luvisolic Order and lie within the Gray Luvisol soil zone. Generally they have light-coloured, eluvial Ae horizons above illuvial Bt horizons that contain silicate clay (C.S.S.C. 1978). Mineral soils have developed from glacial till and have properties that fall within the limits of the Cooking Lake and Uncas soil series (Crown 1977). They are arranged in a catenary sequence. Well to moderately drained Orthic Gray Luvisol soils occupy upper and middle slopes. Dark Gray Luvisol soils are found on less densely treed, more open areas. A small proportion of Eluviated Eutric Brunisol soils are also present (Crown 1977). Imperfectly drained Gleyed Gray

Luvisol soils occupy lower slopes while poorly drained Humic Luvic Gleysol soils occupy depressional, low-lying and interridge areas. Surface texture may be loam to silt loam or sandy loam to loamy sand. Landform is generally ridged to hummocky with slopes of 5 to 15 percent.

Very poorly drained organic soils occupy depressional, low-lying areas and lake margins. Their properties fall within the limits of the Stebbing and St. Lina soil series (Crown 1977). Dominant soils of the former series are Typic Fibrisols that have developed on fibric organic materials, predominantly moss peat. Sub-dominants are Mesic Fibrisols and Terric Mesic Fibrisols. These soils have developed in level bogs. Dominant soils of the latter series consist of Terric Mesisols; sub-dominants include Typic Mesisols, Humic Luvic Gleysols and Humic or Rego Gleysols. These soils, found either in open wetlands or marshes, have developed on moderately decomposed organic material, chiefly derived from sedges, and grasses or cattails.

G. Flora

The Cooking Lake Moraine represents an isolated island of the Mixedwood Section surrounded by the Aspen Grove Section of the Boreal Forest Region (Rowe 1972). The dominant tree species of the Mixedwood Section is aspen

(*Populus tremuloides*)[3] with balsam poplar (*P. balsamifera*) on more moist sites, white birch (*Betula papyrifera*) and black spruce (*Picea mariana*) in boggy areas (Moss 1932). Vestiges of white spruce (*Picea glauca*), thought to be the climax species before the fires of 1895, occur sporadically in protected areas.

The aspen understory includes prickly rose (*Rosa acicularis*)[4] and beaked hazelnut (*Corylus cornuta*), as well as saskatoon (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*) and wild red raspberry (*Rubus strigosus*). The herb layer includes marsh reed grass (*Calamagrostis canadensis*) and numerous forbs such as asters (*Aster* spp.), goldenrods (*Solidago* spp.), etc. found growing on Gray Luvisol soils.

More open, south-facing slopes are vegetated by buckbrush (*Symphoricarpos occidentalis*) and wild rose. Grasses such as fringed brome (*Bromus ciliatus*), Kentucky bluegrass (*Poa pratensis*), bearded wheatgrass (*Agropyron subsecundum*), and various forbs comprise these grassland areas which are underlain by Dark Gray Luvisol soils. Low-lying, poorly drained depressional areas consist of bogs, fens and marshes. Bogs characteristically support stands of swamp birch, (*Betula glandulosa*), white birch, and/or black spruce with an understory of Labrador tea (*Ledum groenlandicum*), blueberry (*Vaccinium myrtilloides*), cloudberry (*Rubus chamaemorus*) and moss (*Sphagnum* spp.). The sedges *Carex aquatilis, C. atherodes* and *C.rostrata* occupy the wettest sites of fens. Drier sites are occupied by willows including *Salix bebbiana, S. discolor, S. petiolaris, S. planifolia, S. maccalliana* and *S. pyrifolia*, with an understory of grasses, particularly marsh reed grass, and forbs. Marshes are bordered by cattails (*Typha latifolia*), rushes (*Juncus* spp.) and sedges (*Carex* spp.).

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[3] Scientific names of vascular plants follow Moss (1959).
[4] Includes *R. woodsii*.

H. Fauna

A rich and varied fauna exists in the study area due to the diversity of habitats (Griffiths 1979). Especially prominent though infrequently seen were the large herbivores: elk, moose and white-tailed deer. These animals were most often encountered while bedded down or foraging in shrub meadows or sedge fens. During this study the porcupine (*Erethizon dorsatum*) was usually seen barking the upper branches of willows, while the red squirrel (*Tamiasciurus hudsonicus*) was noted in black spruce bogs. Presence of Richardson's pocket gopher (*Thomomys talpoides talpoides*), was evidenced by numerous dirt mounds on open areas, but the animal itself was rarely seen. Beaver and muskrat (*Ondatra zibethicus*) were frequently observed in lakes. Occasionally the coyote (*Canis latrans*) and the striped skunk (*Mephitis mephitis*) were seen in the woods or along trails. Other small mammals seen occasionally were snowshoe hare (*Lepus americanus*), weasel (*Mustela* spp.), mink (*Mustela vison*) and little brown bat (*Myotis luciugus*). A large number of bird species were also observed throughout the field season.

III. Methods

A. Aerial Stratification and Mapping

Initially, black and white aerial photographs (Government of Canada: Energy, Mines and Resources - 1972; approximate scale:- 1:12,000) were acquired to obtain an overview of the study area and for use in the preparation of a vegetation cover map. The purpose of the map was to facilitate random plot selection, and to calculate and compare the area of each major vegetation type. With the aid of a stereoscope the area was stratified into four cover types based on drainage, and differences in vegetation structure, as determined from colour tones and textural differences visible on the photos: forest, shrub fen, grass-sedge fen and grassland. Boundaries of each cover type were then transcribed from the individual photos onto a transparent mylar overlay which was enlarged 2X by means of a zoom transferscope. From the mylar overlay ozalid copies were made upon which each cover type was colour-coded, then subdivided into numbered stands. The area of each stand was determined by an electronic digitizer, and totalled, to give the area of each cover type.

B. Stand Selection and Plot Establishment

Forest and Shrub Fen

Ten and twelve stands in each of forest and shrub fen cover types respectively, were selected by using a table of random numbers, and were located during April and May, 1977. The location for a 30 X 30 m macroplot was selected near the centre of each stand (Figure 2). Four 15-metre-long transects were then layed out, one in each cardinal direction. The centres of 12 microplots[5] (Figure 2) individually spaced at five metre intervals, were located along each transect, marked with a wooden stake and numbered. A compass placed at each centre in turn, served to divide the microplot into four imaginary quadrants, each of which was designated with a Roman numeral.

Grassland and Grass-Sedge Fen

Eight grassland stands were subjectively chosen which best represented the grassland cover type. Four, 0.89 m^2 microplots in three stands, and six microplots in two stands, were located and equally distributed among grassy and shrubby phases of the grassland during May, 1977. A wire exclosure cone having approximately the same basal area as each microplot was placed over the centre of each plot.

Ten stands were chosen by means of a table of random numbers in the grass-sedge fen during August, 1977, to assess herbaceous forage yield. A 25 m transect was run in each cardinal direction from a point central to each of five stands of *Calamagrostis canadensis* and five stands of *Carex* spp. Five, 0.89 m^2 plots were placed at five metre intervals along each transect.

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[5] Referred to as sample points according to Cottam and Curtis (1956).

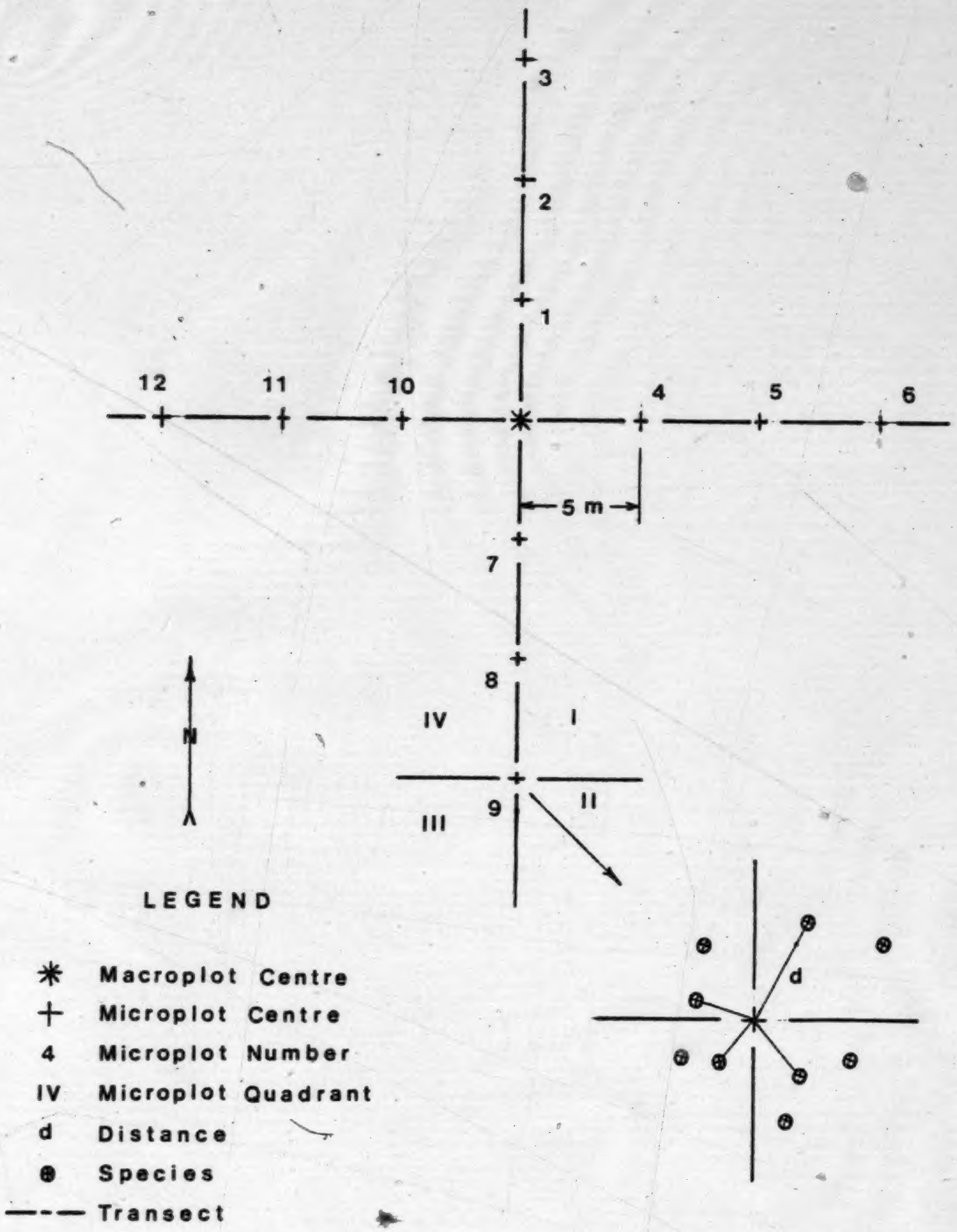

Figure 2. A macroplot and its number and arrangement of microplots.

C. Species Composition

Herbaceous Vegetation

Following Daubenmire (1959), canopy cover was determined in each microplot for each herbaceous species, and for woody vegetation less than or equal to 61 cm tall. Daubenmire (op cit.) defined canopy cover as: "an expression of the percentage of the ground included in a vertical projection of imaginary polygons, drawn about the total natural spread of foliage of the individuals of a species." A 20 X 50 cm plot frame was used as the microplot. The coverage classes and mid-points are given below:

Class No.	Range in Cover(%)	Mid-Point(%)
1	0-1	1
2	2-5	3
3	6-25	15
4	26-50	38
5	51-75	62
6	76-95	85
7	96-100	98

The plot frame was placed at a predetermined, randomly selected[6], distance and direction from the centre of each microplot.

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[6] From a table of random numbers.

Woody Vegetation

The point-centred quarter method (Cottam and Curtis 1956) was used to obtain an inventory of woody vegetation[7] which was greater than 61 cm in height and less than 3.75 cm diameter at breast height (dbh). The method was modified for clumped vegetation[8] (i.e. *Salix* spp.), since it tends to give an underestimate of individuals in a population which is contagiously distributed (Mueller-Dombois and Ellenberg 1974). It was felt that this modification would give a better estimate, since all stems in a clump would be considered. The shortest distance from the microplot centre to the nearest stem (or clump if applicable) in each quarter, as well as its height, basal diameter and species name were recorded.

The basal area of a stem was calculated by multiplying its basal diameter by 3.1416. The basal area of a clump was calculated by multiplying the average basal area of two stems, (one nearest the clump centre, the other nearest the microplot centre), by the number of stems per clump.

The height and dbh of three trees nearest the centre of each macroplot were measured as representative of stand height (Appendix B). A 10-factor prism was used to estimate basal area for trees within seven dbh size classes ranging from 3.8 to 39.4 cm with a size class interval of 5 cm.

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[7] Two species, *Rubus strigosus* and *Lonicera* spp., were regarded as a type of cane rather than a typical woody species . Hence, they were not included as such in this inventory but were included in the canopy cover method for herbaceous forage.

[8] The distance to the centre of each clump, as opposed to each stem, was measured. Then the number of stems were counted in each clump.

D. Production and Utilizatio[illegible]

Herbaceous Vegetation

Grassland

Current annual growth (CAG) and use of herbaceous forage and browse ($\leq$61 cm in height), was determined by harvesting (Stoddart et al. 1975) during August. Twenty-four wire exclosure cones, approximately 120 x 106 cm basal diameter, were placed in five grassland stands at the point where a tossed stick landed. One half of the cones were placed in the grassy phase[9] while the other half were placed in the shrubby phase. Each cone was secured by three U-shaped stakes.

Herbaceous forage was clipped to ground level within a 0.89 m^2 plot frame inside and outside of each wire cage during peak production near the latter part of August. This material as well as ground litter was collected and later sorted into grasses and grasslikes, forbs and litter. CAG of woody species found within the plot was also clipped and collected, and sorted into leaves and twigs. All this material was air-dried for several days at room temperature, placed in a forced-air oven for 24 hours at 70°C then weighed. Herbaceous forage and woody material collected during April of the following spring was treated in the same manner.

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[9] The grassland community consisted of a shrubby part near the perimeter, as well as a grassy part nearer the centre, hence two phases.

Grass-Sedge Fen

The production of herbaceous annual growth was also determined by the clip-plot method for lowland meadows. Ten stands were randomly chosen using a table of random numbers. The circular plot frame was positioned at five metre intervals along a subjectively placed transect line in five sedge dominated, and five marsh reed grass dominated communities. Forage from five plots in each of these communities was clipped and collected during August. This material was then air-dried, oven-dried and weighed in the same manner as for grassland forage.

Woody Vegetation

Forest and Shrub Fen

Current annual growth and use of browse was determined from approximately mid-April to mid-May by means of the twig-count method (Shafer 1963) and the twig diameter-weight relationship method (Telfer 1969). In the former method, the number of browsed and unbrowsed twigs[10] of important browse species was tallied for stems previously tagged at each of the points in the point-centred quarter survey. In the latter method, the diameter of current growth (DCG) and the diameter at point of browsing (DPB) were measured with a vernier caliper for several twigs on various stems in each microplot; approximately 175-200 total twig measurements per species. These measurements were also recorded for several unmarked stems of scarce browse species whenever they were encountered to bring their totals up to 200. Standardized twig diameter-weight relationships, previously calculated for each important browse species[11], were then applied to these measurements to estimate the yield and use of each species. Total yield per species was calculated by multiplying mean twig weight (extrapolated from mean DCG) X mean number of twigs per stem X mean number of stems per ha. Total use per species was calculated by multiplying mean twig weight (extrapolated from mean DPB) X mean number of browsed twigs per stem X mean number of stems per ha. Percent use was determined by dividing total use by total yield X 100.

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[10] Twigs ≤3.75 cm in length were considered too short to be browsed by ungulates and so were not counted.

E. Chemical Composition

Forage Collection

Material for analysis of the chemical composition of forage was collected in the following manner: a 600-800 gm sample of herbaceous material was collected from each of six, widely spaced, grassland and sedge fen cover types during the months of June and July. A sample of CAG from different locations on five or six plants of each of nine important browse species, was similarly collected during June and July, and December and March, from the forest and shrub fen cover types. Four of six samples in each of the herbaceous and woody material were sorted into grass, sedge, forb, litter; and leaf and twig categories respectively, and air-dried in paper bags for several days at room temperature. A sub-sample of 100-150 gm was placed in a plastic bag for storage and later chemical analysis.

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[11] Appendix A.

Chemical Analysis

The chemical analysis of forage was conducted at the forage quality laboratory, Department of Plant Science, University of Alberta. Paired, pooled samples of each class and species of forage were analyzed for nitrogen, ADF (acid-detergent fibre), ADL (acid-detergerent lignin), calcium, phosphorus and ash. Nitrogen content was determined by the Dumas method, using the Coleman 29A nitrogen analyzer. A conversion factor of 6.25 was used to convert percent nitrogen to percent crude protein (Maynard and Loosli 1969). ADF and ADL were obtained by the procedure described by Van Soest (1963a and 1963b). Total ash was determined by the combustion of a 0.5 gm sample in a muffle furnace, following a method described by Isaac and Jones (1972). Calcium and phosphorus were obtained by using the Technicon Auto-Analyzer following methods of the A.O.A.C. (1975).

F. Mathematical and Statistical Analysis

The relative importance or prominence (P) of herbaceous species was determined by the formula: $P = \%C \times \sqrt{\%F/100}$, where P=prominence index; C=percent cover; F=percent frequency (Pinchbeck pers comm.)[12]. This formula provides an index of importance based on cover and frequency, and is essentially a frequency weighted cover. That is, it increases in importance, species with high frequency-low cover, and decreases in importance, species with low frequency-high cover. A principle components analysis (Overall and Klett 1972), was used to verify the physiognomic classification. A hierarchical cluster analysis method (Wishart 1978), was used to group stands which were relatively similar into plant communities. Means and standard errors were calculated for yield, use and chemical composition data of forage classes and species (Snedecor and Cochran 1967). Paired and unpaired t-tests at the 1 and 5 percent level were used to test for significance in yield and use of browse and herbaceous forage by year, forage class and species. A one-way analysis of variance and the Student-Newman-Kuels multiple range test at the 1 and 5 percent level were used to test for significance of chemical composition data, by forage class and species. An unpaired t-test was used to test for seasonal differences in chemical composition of twigs. Chi square and the Bonferroni *z* statistic were used to determine whether there was significant preference among browse species. Hotelling's T-squared and the F-statistic were used to test if preference was correlated with chemical composition.

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[12] Pinchbeck, B. March, 1979, personal communication.

IV. Communities

A. Results

Ordination

Species

A two-dimensional ordination based on the field layer accounted for approximately 23% of the variation (Figure 3). *Poa pratensis* and *Calamagrostis canadensis* were most highly associated with the driest and wettest extremes respectively, of a moisture gradient running from left to right along the X-axis. The grouping of several other species nearer the ends of this axis indicated further, their association with a dry or wet environment. Nearer the centre, *Populus balsamifera* indicated intermediate moisture, while left of centre, *Aster laevis* indicated a comparatively dry moisture regime.

Aralia nudicaulis was the species most highly associated with the Y-axis which represented a decrease in light intensity upward (Figure 3). Other shade-tolerant species such as *Maianthemum canadense*, *Rubus pubescens*, *Cornus canadensis* and *Mertensia paniculata*, grouped near the upper end of this axis, symbolized low light intensity resulting from closed tree canopy. Six species scattered along the Y-axis indicated a change in light intensity and moisture, and therefore represented an ecotone between forest and grassland. *Lathyrus ochroleucus* and *Rubus strigosus* appear to be associated more with low light

Species

Code	Scientific Name
Arnu	*Aralia nudicaulis*
Rupu	*Rubus pubescens*
Maca	*Maianthemum canadense*
Cocn	*Cornus canadensis*
Mopa	*Mertensia paniculata*
Laoc	*Lathyrus ochroleucus*
Rust	*Rubus strigosus*
Frvi	*Fragaria virginiana*
Viam	*Vicia americana*
Rosa	*Rosa acicularis*
Thve	*Thalictrum venulosum*
Taof	*Taraxacum officinale*
Gabo	*Galium boreale*
Sosp	*Solidago species*
Syoc	*Symphoricarpos occidentalis*
Acmi	*Achillea millefolium*
Agsu	*Agropyron subsecundum*
Poap	*Poa pratensis*
Brci	*Bromus ciliatus*
Anca	*Anemone canadensis*
Asle	*Aster laevis*
Poba	*Populus balsamifera*
Caro	*Carex rostrata*
Caat	*C. atherodes*
Caaq	*C. aquatilis*
Imca	*Impatiens capensis*
Eqar	*Equisetum arvense*
Gate	*Galeopsis tetrahit*
Aspu	*Aster puniceus*
Pesg	*Petasites sagittatus*
Popl	*Potentilla palustris*
Gatr	*Galium trifidum*
Mear	*Mentha arvensis*
Scga	*Scutellaria galericulata*
Cacn	*Calamagrostis canadensis*

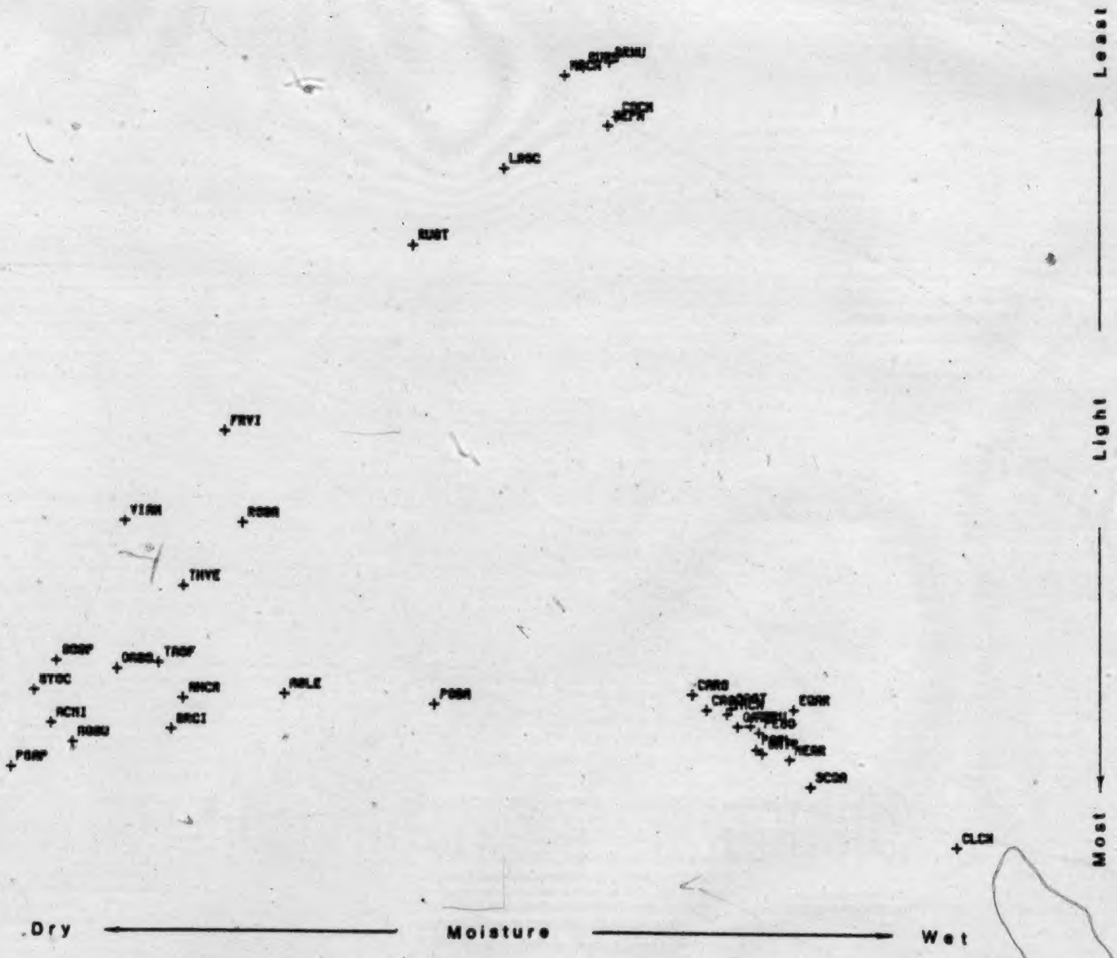

Figure 3. Ordination of species on the 1st and 2nd principle components (X - Y axes).

intensity and intermediate moisture, while *Fragaria virginiana*, *Vicia americana*, *Rosa acicularis* and *Thalictrum venulosum* are associated with drier, more open situations.

Ordination of species along the first and third dimension (X-Z axes) accounted for 14% of the variation (Figure 4). The Z-axis, representing the period of inundation, separated wetland species into two distinct groups. *Potentilla palustris* was associated most highly with the uppermost group along the Z-axis which was also characterized by less highly associated *Galium trifidum*, *Carex aquatilis* and *C. atherodes*. The remaining wetland species near the bottom end of the axis characterized the second wetland group. *Scutellaria galericulata* positioned mid-way between the two groups represented an ecotonal situation.

Stands

A two-dimensional ordination of 40 stands based on the field layer is illustrated in Figure 5. The stands are distributed in three distinct groups; two along the X-axis and one along the Y-axis. Two groups of eight and 22 stands, near the left and right ends of the X-axis, indicate the dry and wet extremes respectively, of the moisture gradient. The 22 stands of the wetland area are relatively similar, as illustrated by their close proximity to one another. Six of eight stands are comparatively similar in the dry area, since stands 301 and 311 are relatively distant from one

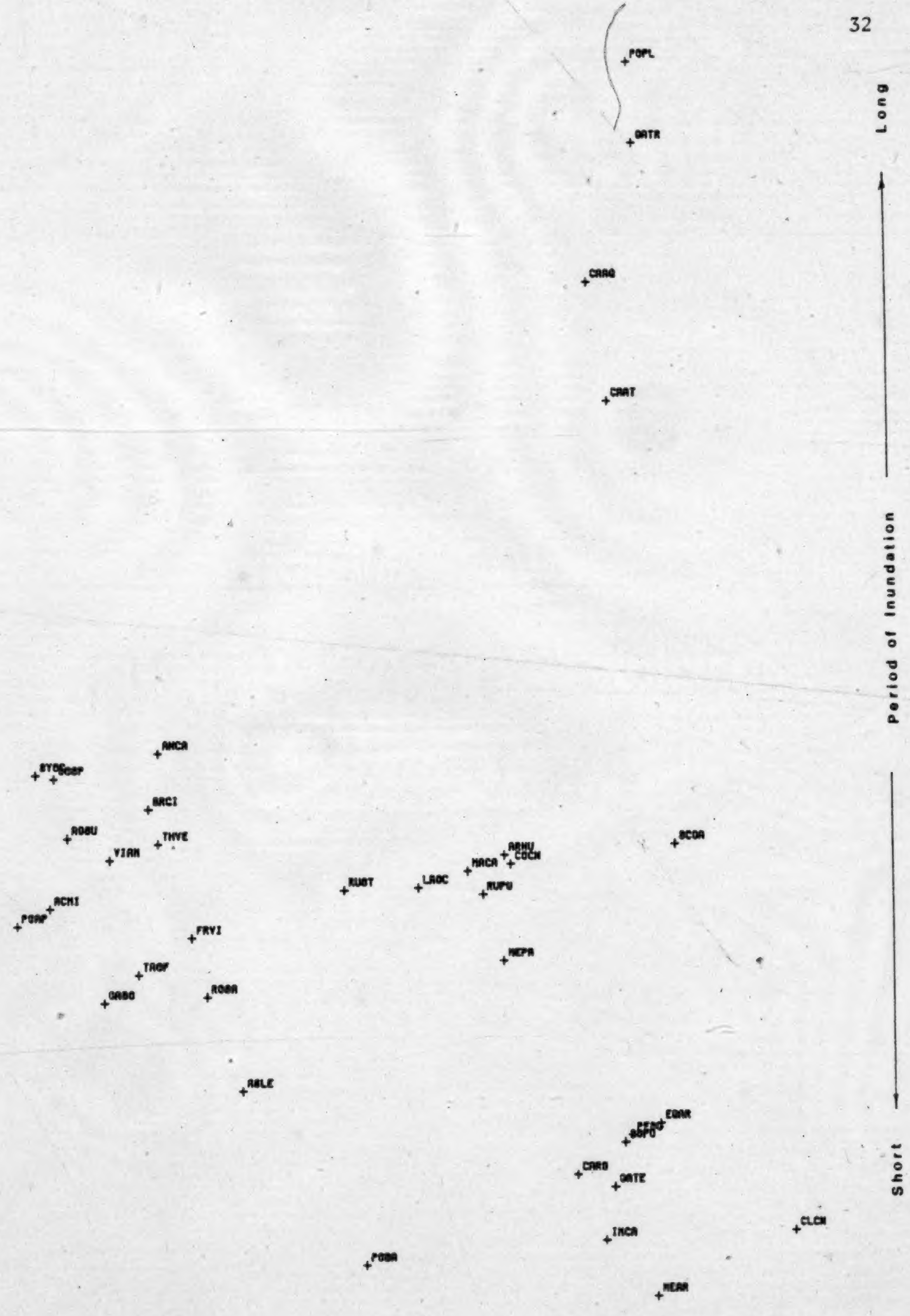

Figure 4. Ordination of species on the 1st and 3rd principle components (X - Z axes).

Stand Numbers

Forest

1110
1136
1148
1152
1155
1159
1170
1179
1206
1228

Grassland

3301
3305
3311
3356
3367
3369
3370
3390

Shrub Fen

2503
2506
2508
2511
2534
2544
2555
2548
2563
2603
2604
2605

Grass-Sedge Fen

4306
4307
4318
4330
4342
4336
4351
4353
4401
4435

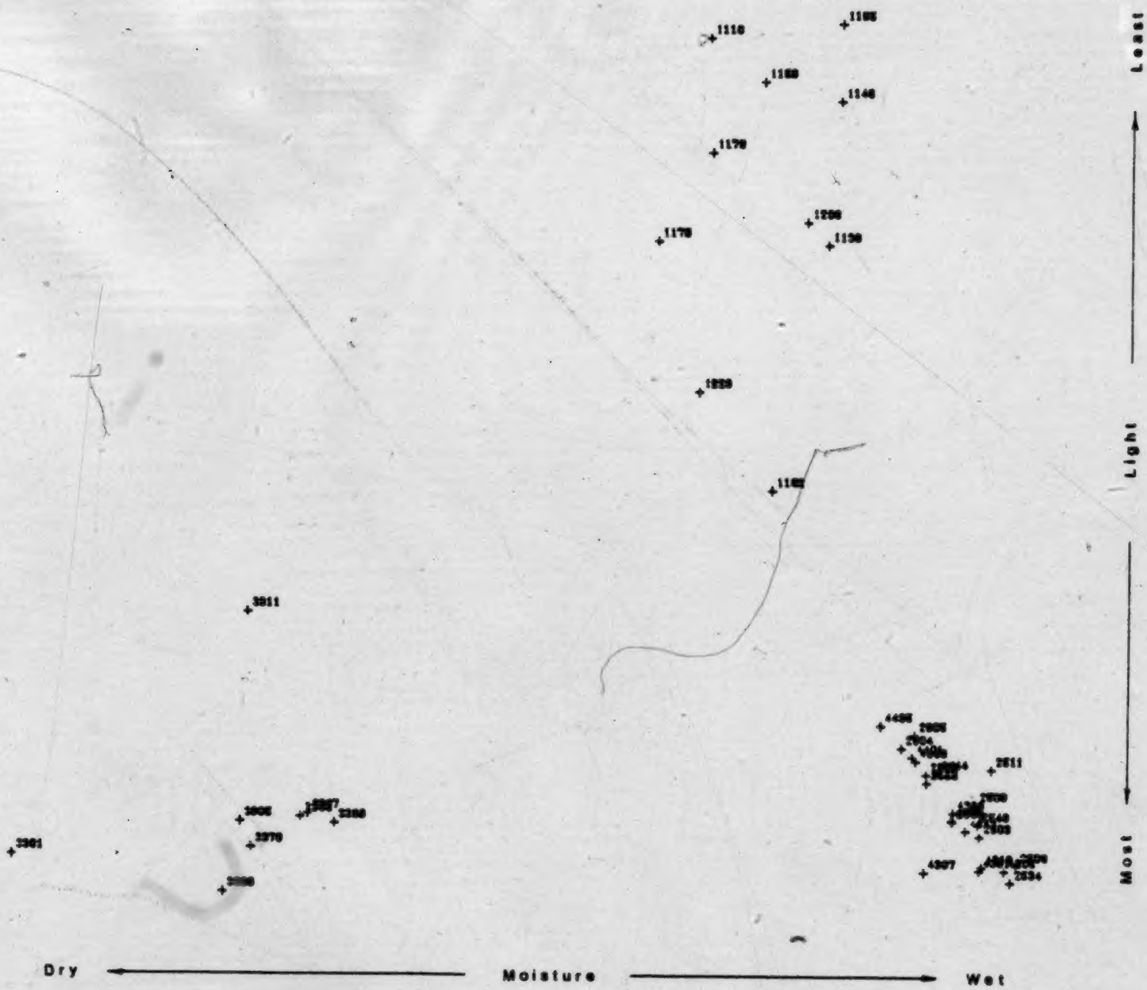

Figure 5. Ordination of stands on the 1st and 2nd principle components (X - Y axes).

another and the remaining six stands. Stands which comprise the third group along the Y-axis, are relatively dissimilar as illustrated by their wide spacing.

The X-Z axes illustrate the separation of wetland stands into two distinct groups (Figure 6). The uppermost group consists of three stands, two of which are very similar, but distinct from the third stand. The lowermost group consists of 19 stands. The close proximity of some stands within these groups illustrates their similarity, but overall, this group is highly variable.

Cluster Analysis

A cluster analysis of the 40 stands and the resultant dendrogram, illustrate the association between stands and their relationship to the four communities (Figure 7). The first and most obvious level of separation was between the eight stands of the grassland community and the remaining 32 stands of the non-grassland community. The distinguishing feature of the grassland stands was the predominance of *Poa pratensis*, the dominant species in five stands (Appendix F). Other major species included *Bromus ciliatus, Agropyron subsecundum, Galium boreale, Achillea millefolium, Taraxacum officinale* and *Solidago* spp. Another attribute of the grassland stands was the presence of *Symphoricarpos occidentalis*, the dominant shrub.

At the second level of separation, the 32 stands of the non-grassland community were subdivided into 10 and 22 stands of the forest and wetland communities, respectively

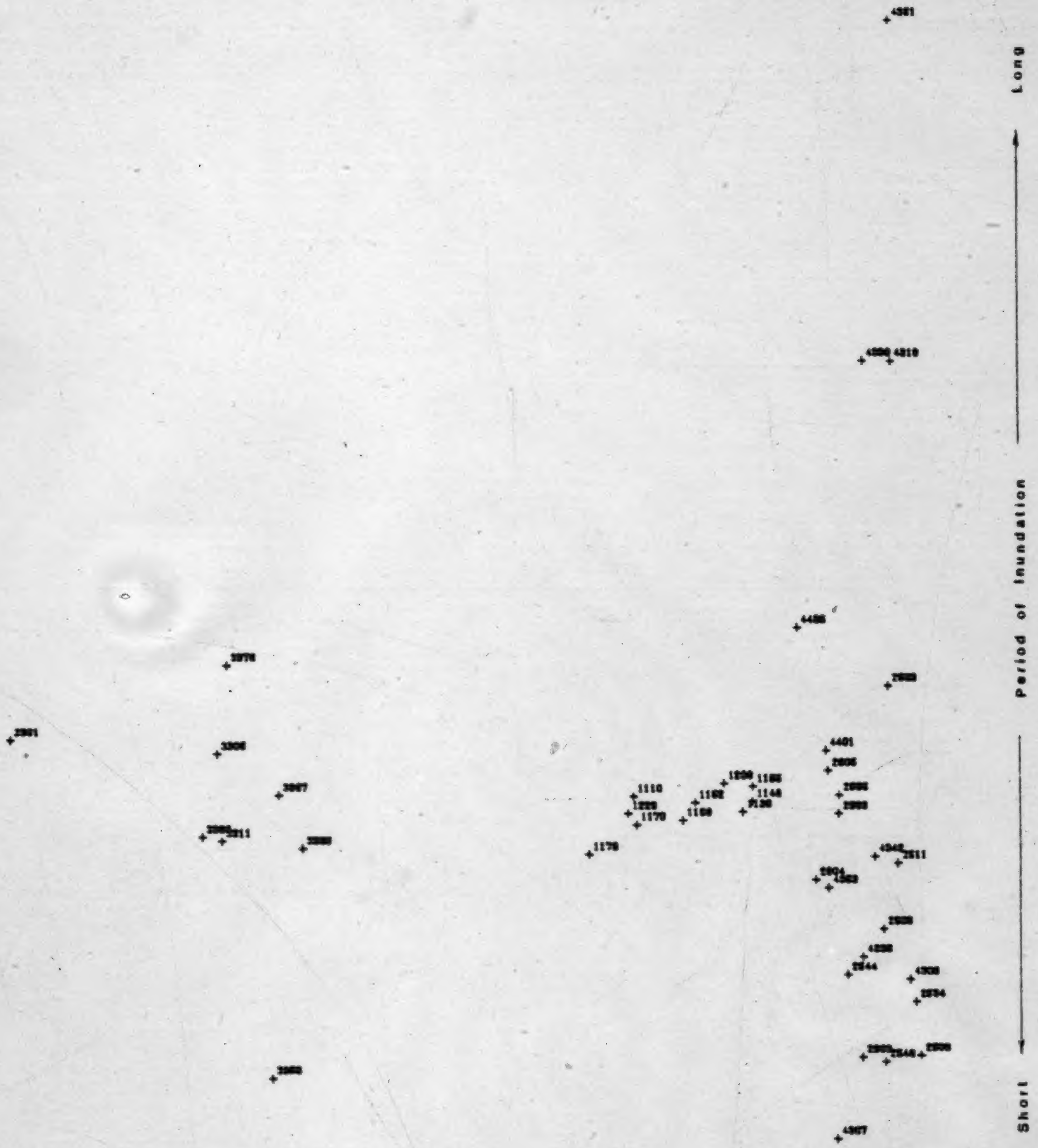

Figure 6. Ordination of stands on the 1st and 3rd principle components (X - Z axes).

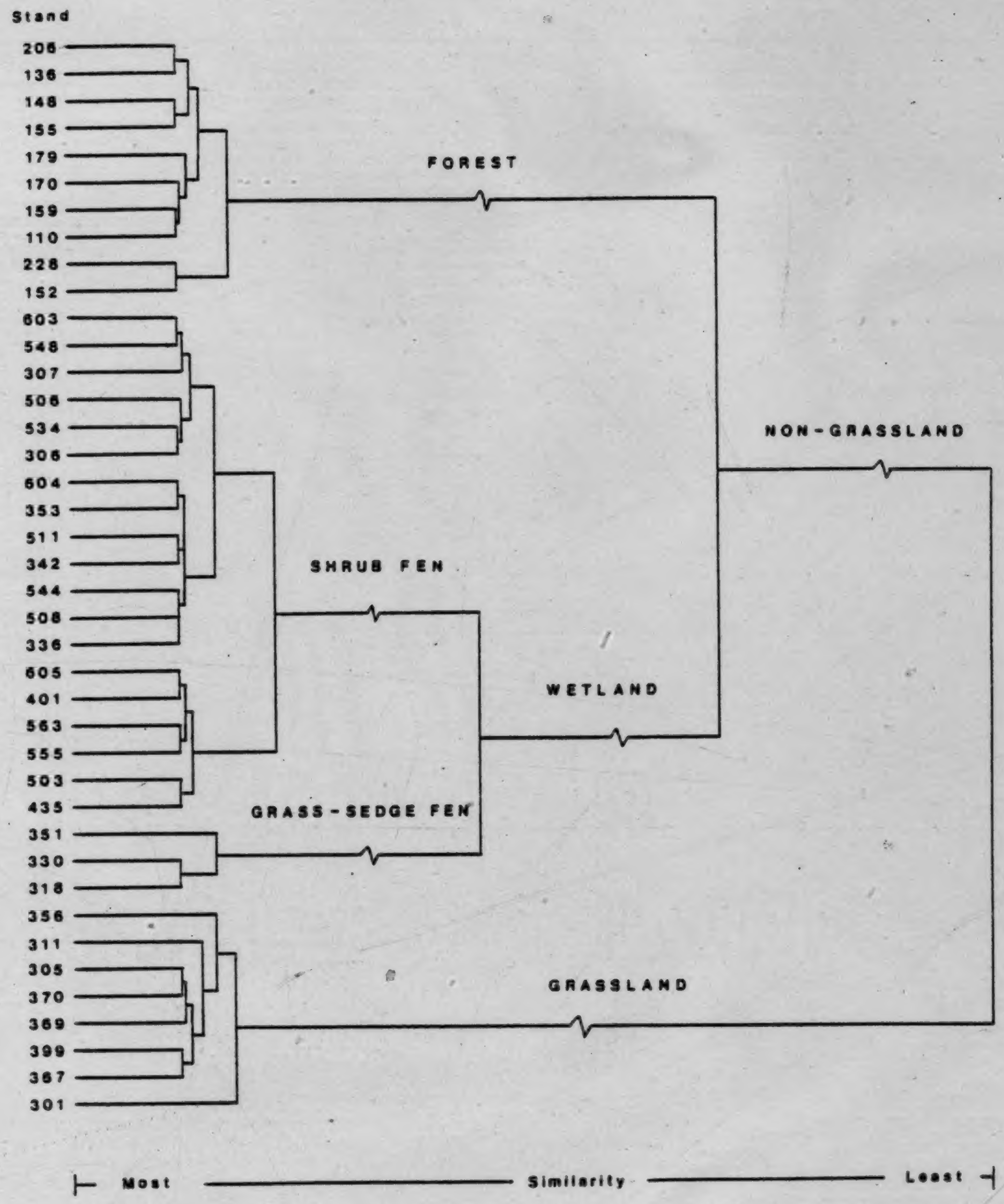

Figure 7. Dendrogram of the 40 stands of the forest, shrub fen, grass-sedge fen and grassland plant communities.

(Figure 7). *Aralia nudicaulis* was the most distinctive species of the forest community where it occurred as the dominant in six stands (Appendix C). Other distinctive species included *Rubus pubescens*, *Calamagrostis canadensis*, *Lathyrus ochroleucus*.

The third level of separation illustrates a subdivision of the wetland community into 19 shrub fen stands and three grass-sedge fen stands (Figure 7). The distinctive species of the shrub fen community is *Calamagrostis canadensis*, dominant in all except three stands (Appendix G). Less characteristic species were *Carex atherodes* and *C. rostrata*, dominants in two and one stands respectively; and *Equisetum arvense* and *Scutellaria galericulata*.

Three stands were characteristic of the sedge fen community (Figure 7). *Carex atherodes* was the dominant sedge in two stands, while other typical species included *Potentilla palustris*, *Galium trifidum*, *Carex aquatilis* and *Calamagrostis canadensis* (Appendix H).

Classification and Description

Forest (*Populus-Aralia*) Community

Populus tremuloides was the sole dominant tree species in the forest community (Plate 1). Its presence set the forest community apart from the other communities. Average tree height, basal area and dbh are given in Appendix B. The

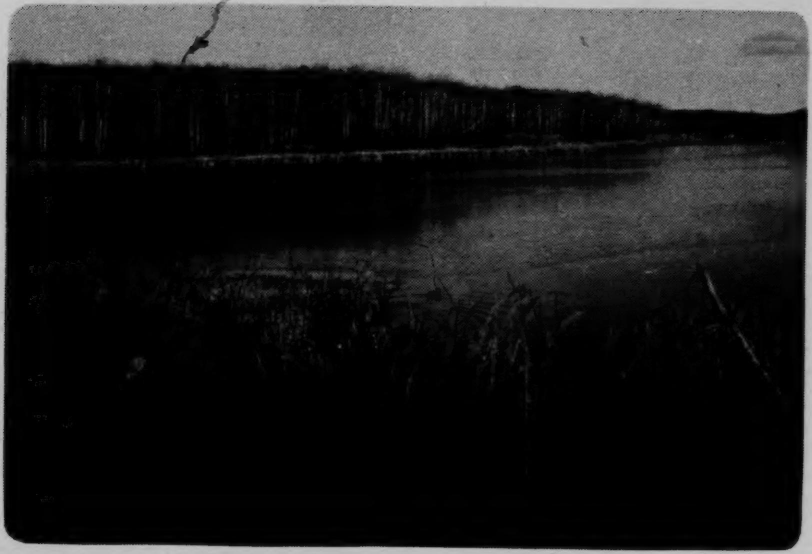

Plate 1 The forest plant community (and Walter Lake) as seen from afar (above), and from within (below), showing the dense understory of shrubs.

two co-dominant shrubs in the tall shrub layer (≥61 cm)[13] were *Rosa acicularis* and *Corylus cornuta* (Table 2). *Amelanchier alnifolia*, *Populus tremuloides* and *Prunus virginiana* were much less important than the co-dominants. Of these three species, *Amelanchier alnifolia* was the most important, having a density and frequency greater than either *Populus tremuloides* or *Prunus virginiana*, but a dominance value greater only than that of *Prunus virginiana*. In the low shrub layer (≤61 cm) there was nearly equal importance in *Rubus strigosus*, *Symphoricarpos occidentalis*, and *Rosa acicularis* (Table 2; Appendix C). The dominant herb was *Aralia nudicaulis* which had prominence and cover values approximately three and four times greater than those of *Rubus pubescens*, *Calamagrostis canadensis*, *Lathyrus ochroleucus* and *Maianthemum canadense*, respectively. Other species in order of decreasing importance included *Mertensia paniculata*, *Fragaria virginiana*, *Galium boreale*, *Cornus cornuta*, *Vicia americana*, *Solidago* spp. and *Thalictrum venulosum*. All herbaceous species were relatively evenly distributed.

Shrub Fen (*Salix-Calamagrostis*) Community

The shrub fen community was characterized by an admixture of shrubby and herbaceous vegetation (Plate 2). *Salix planifolia* and *S. pyrifolia* were the most prominant, co-dominant shrubs (Table 2; Appendix D). The density and

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[13] This height is actually related to an average snow depth where shrubs ≥61 cm would be available, and those ≤61 cm would be unavailable.

Table 2. Relative density (%), dominance (%), frequency (%) and importance (%) of shrubs $\geq$ 61 cm in the forest (n = 10) and shrub fen (n = 12) communities.

Species	Forest				Shrub Fen			
	dens[a]	dom[b]	freq[c]	imp[d]	dens	dom	freq	imp
Rosa acicularis	43	29	20	92				
Corylus cornuta	31	40	16	86	+	+	1	1
Amelanchier alnifolia	12	9	20	41	+	+	1	1
Populus tremuloides	7	16	10	33	12	+	10	21
Prunus virginiana	5	3	16	24				
Salix discolor	+[e]	+	4	6	6	7	11	24
Populus balsamifera	+	+	2	3	2	+	5	7
Salix bebbiana	+	+	2	3	4	+	12	17
Ribes oxyacanthoides	+	+	2	3	5	+	8	13
Cornus stolonifera	+	+	2	2	+	+	1	1
Betula papyrifera	+	+	2	2	15	+	8	24
Viburnum edule	+	+	2	2				
Other *Ribes* spp.	+	+	2	2	2	+	6	8
Salix planifolia					28	31	13	72
S. pyrifolia					11	48	8	67
S. maccalliana					12	8	6	26
S. petiolaris					3	4	7	15
Lonicera spp.					+	+	1	2
Alnus spp.					+	+	+	+

[a] Relative density - $\frac{\text{Number of individuals of species}}{\text{Total number of individuals}} \times 100.$

[b] Relative dominance - $\frac{\text{Total basal area of species}}{\text{Total basal area of all species}} \times 100.$

[c] Relative frequency - $\frac{\text{Number of points of occurrence of species}}{\text{Occurrence of all species}} \times 100.$

[d] Importance value - Relative density + relative dominance + relative frequency.

[e] Refers to a value of < 1%.

Plate 2 The shrub fen plant community showing willow clumps in a matrix of grass and sedge vegetation.

frequency of *S. planifolia* was considerably greater than that of *S. pyrifolia* while the opposite was true for dominance. *S. maccalliana, S. discolor, Betula papyrifera* and *Populus tremuloides* were much less important but relatively similar to one another. *S. maccalliana* and *Populus tremuloides*, the most and least important of the latter four species, were equally as dense but differed markedly in frequency and dominance. *Betula papyrifera* and *S. discolor* were equally as important but opposites in density, dominance and frequency.

Grass-Sedge Fen (*Calamagrostis-Carex*) Community

Calamagrostis canadensis was the dominant species of the grass-sedge fen community (Plate 3) where it was evenly distributed and had the highest cover value of all species (Table 3; Appendix E). *Carex atherodes* was relatively unevenly distributed but this was offset by its high cover value wherever it occurred. Much less dominant but approximately equal in importance were *Carex aquatilis, Potentilla palustris, Equisetum arvense* and *Scutellaria galericulata*. *Scutellaria galericulata* was most evenly distributed and had the lowest cover while the opposite was true for *Carex aquatilis*. *Potentilla palustris* and *Equisetum arvense* were very similar with respect to distribution and cover.

Grassland (*Poa-Symphoricarpos*) Community

The most prominent species characteristic of the grassland community (Plate 4) was *Poa pratensis* (Table 2;

Plate 3 The grass-sedge fen plant community showing sedge vegetation in the centre and marsh reed grass near the edge.

Table 3. Average cover (%), frequency (%) and prominence of important[a] species in the forest (n = 10), shrub fen (n = 12), grass-sedge fen (n = 10) and grassland (n = 8) communities.

	Forest			Shrub Fen			Grass Fen			Grassland		
Species	c[b]	f[c]	p[d]	c	f	p	c	f	p	c	f	p
Woody ($\leq$ 61 cm)	3	90	3							2	50	1
Rubus strigosus	3	90	3							2	50	1
Symphoriearpos occidentalis	3	100	3							16	100	16
Rosa acicularis	2	80	2							4	87	4
Amelanchier alnifolia	1	60	1									
Viburnum edule	2	60	1									
Lonicera involucrata				2	58	1						
Herbaceous												
Aralia nudicaulus	29	90	27									
Rubus pubescens	10	100	10									
Calamagrostis canadensis	9	100	9	53	100	53	56	90	54	2	37	1
Lathyrus ochroleucus	9	100	9									
Maianthemum canadense	7	100	7									
Mertensia paniculata	4	100	4									
Fragaria virginiana	3	100	3							6	100	6
Galium boreale	3	100	3							17	100	17
Cornus canadensis	3	80	2									
Vicia americana	2	80	2							6	100	6
Solidago spp.	2	70	2							14	87	13
Thalictrum venulosum	1	80	1							3	87	3
Equisetum arvense				8	75	7	3	60	2			
Carex atherodes				6	67	5	28	40	18			
Scutellaria galericulata				4	75	3	2	90	2			
Mentha arvensis				2	100	2	2	50	1			
Impatiens capensis				2	92	2						
Aster puniceus				2	75	2						
Carex rostrata				4	25	2	2	40	1			
Galeopsis tetrahit				3	42	2						
Arennaria spp.				2	58	1						
Unknown sp. *f*				3	25	1						
Carex aquatilis							6	20	3			
Potentilla palustris							3	50	2			
Galium trifidum							2	60	1			
Petasites sagittatus							2	50	1			
Poa pratensis										41	100	41
Agropyron subsecundum										20	88	19
Achillea millefolium										17	100	17
Bromus ciliatus										16	100	16
Taraxacum officinale										10	88	9
Aster laevis										6	100	6
Anemone canadensis										6	75	5
Trifolium repens										3	63	2
Artemisia ludoviciana										4	25	2
Calamogrostis neglecta										2	25	1
Agastache foeniculum										1	100	1

[a] Important species are those having a pi $\geq$ 1.

[b] Average cover - mean over all plots.

[c] Frequency - % of the plots in which species occurred.

[d] Prominence index - average % cover × $\sqrt{\%\ \text{frequency} \div 100}$

Plate 4 The grassland plant community showing the grassy phase (foreground) and the shrubby phase (background).

Appendix F). *Agropyron subsecundum* was also a prominent species, even though its cover and prominence index were slightly less than half those of *Poa pratensis*. *Galium boreale* and *Achillea millefolium*, with essentially the same distribution and cover, and *Bromus ciliatus*, were all slightly less prominent than *Agropyron subsecundum*. Other minor species in order of decreasing importance included *Solidago* spp., *Taraxacum officinale*, *Aster laevis*, *Fragaria virginiana* and *Vicia americana*. *Symphoricarpos occidentalis* was the dominant shrub, with *Rosa acicularis* and *Rubus strigosus* somewhat less important.

The grassland community actually consisted of two phases: a grassy phase and a shrubby phase. The grassy phase occupied the centre portion of the grassland. The shrubby phase is a successional stage, occurring between the grassland (grassy phase) and the aspen forest.

The relative association and areal extent of the four major communities are illustrated in Figure 8 and Table 4. The communities are arranged in a complex pattern, characteristic of the Boreal Mixedwood. The forest community occupied the greatest percentage of the total area, approximately 58%. The grass-sedge fen made up approximately 14% of the total area, while the shrub fen and grassland made up 8% and 4% of the area, respectively.

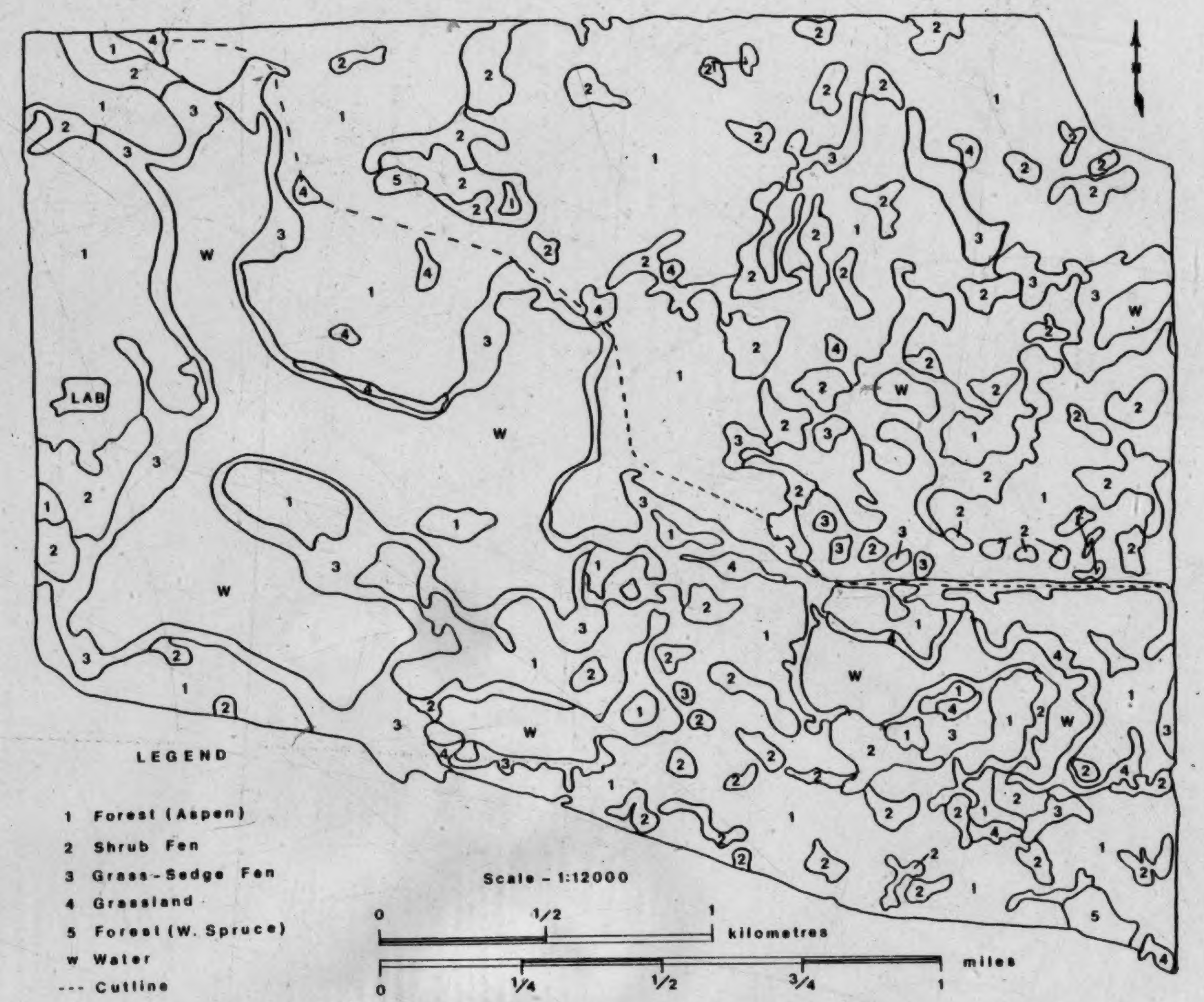

Figure 8. Vegetation map showing the spacial arrangement of the forest, shrub fen, grass-sedge fen and grassland plant communities, and of water.

Table 4. Areal extent of the 4 major communities, and of water, in the study area as determined from 1972 aerial photographs.

Community	ha	%	% (minus water)
Forest [a]	415	58	69
Grass-sedge Fen	97	14	16
Shrub Fen	59	8	10
Grassland	28	4	5
Water	120	17	
Total	723	100	100

[a] Does not include 3 ha of white spruce forest.

B. Discussion

In plant community classification, a number of samples (stands) representing communities are grouped together based on shared characteristics into an abstract unit or class of plant communities (Whittaker 1978). Such units of classification may be referred to as community types. When vegetation samples have been classified into a community type, one may then determine for this type the ranges of environmental factors, species compositions and community characteristics that its samples represent.

Study of communities in terms of gradients of phenomena on the three levels is termed gradient analysis (Whittaker 1967). Samples from plant communities may be arranged in sequence by their positions along a gradient of the environment (or of community characteristics). In this sequence of samples (a transect) changes in species populations and community characteristics are related to changes in the environment. In many cases samples are arranged in relation to a coordinate system of two or more environmental or community gradients. The arrangement allows one to interrelate samples (and species populations) as parts of an abstract pattern of variation in species composition and other characteristics of communities, and to seek understanding of vegetation in relation to the major directions of variation of that pattern.

The process of arranging samples (or species) in relation to environmental gradients or axes is termed ordination (Goodall 1954). Ordination is an essential technique of gradient analysis.

Cluster analysis is another means of vegetation classification whereby samples (stands) are grouped together according to their similarity. The resultant dendrogram illustrates the degree of similarity among stands and thereby allows one to recognize communities and/or community types from similar stand groupings.

Community Classification and Description

Forest, grassland and wetland (shrub fen and grass-sedge fen) were the major community types initially recognized by a subjective, physiognomic approach to the classification of vegetation. These community types were later verified by a second, objective approach to community classification based on the field layer.

The structure and floristic composition of the forest community closely resembled that of the aspen poplar consociation described for central Alberta by Moss (1932). Tree, shrub and herb strata were clearly evident. The tree stratum, dominated by *Populus tremuloides*, formed an almost continuous canopy except where open wetland or grassland areas occurred. However, these areas were often bordered or overgrown by aspen saplings, evidence of forest succession through suckering, also reported by others (Jeffrey 1961; Bailey and Wroe 1974; Sheffler 1976).

Although the tall shrub stratum included the dominants *Amelanchier alnifolia* and *Prunus virginiana*, it did not include *Cornus stolonifera*. The high palatability of this species probably accounted for its scarcity and therefore its lack of dominance. Whereas *Rosa acicularis* and *Corylus cornuta* were co-dominants in the short shrub stratum, Sheffler (1976) reported *Symphoricarpos occidentalis* and *Rosa acicularis* while Moss (1932) reported *Rosa acicularis* and *Rubus strigosus* to be co-dominants. These differences may be explained partially by differences in locality. Also, *Rubus strigosus* was relatively much less prominent because it was considered to be a cane and therefore was eliminated in sampling woody species. Dominant species of the short and tall herb stratum were very similar to those reported by other researchers (Moss 1932; Lynch 1955; Bird 1961; Sheffler 1976).

The grassland community is probably a relict of the once vast northern prairie grassland which, in the absence of fire, has become largely forested by invasion of *Populus tremuloides* (Maini 1960). It is related, geographically and floristically, more to the *Agropyron-Stipa* association than to the *Festuca scabrella* association (Moss 1932; 1955).

The grassland community was also very similar to that which occurs after a poplar forest has been burned, cut or otherwise disturbed (Moss 1932). Such communities were claimed to be seral stages in succession to poplar forest (Moss 1932). Species characteristic of these seres include *Agropyron* spp., *Bromus ciliatus*, *Calamagrostis canadensis*, *Aster* spp., *Solidago* spp., *Epilobium angustifolium*, *Rubus* spp., *Rosa acicularis* and *Symphoricarpos occidentalis*. After two or three years these species are suppressed and replaced by young *Populus tremuloides* and there is a gradual return to the original composition of the community (Moss 1932).

Grazing may delay natural succession indefinitely (Moss 1932; Lynch 1955; Bird 1961). Consequently, shrub, grass or sedge communities commonly arise that are almost stable under the artificial conditions imposed. These communities (socies or associes) may be dominated by *Symphoricarpos occidentalis*, *Salix petiolaris*, *Carex* spp., *Poa palustris*, *P. pratensis* or *Koeleria cristata* (Moss 1932). Since the grassland is dominated by *Poa pratensis* and the shrub *Symphoricarpos occidentalis*, it may be such an associes. Undoubtedly, its stability has been greatly influenced and maintained through grazing by the ungulate and rodent population, and by topographic position and drainage. However, the predominance of *Symphoricarpos occidentalis* suggests its invasion of the grassland, a fact which is characteristic of the zone between grassland and aspen forest (Pelton 1953; Bailey and Wroe 1974; Sheffler 1976; Wheeler 1976).

The wetland community type was characterized by marsh (grass-sedge fen) and swamp (shrub fen) formations, as opposed to bogs (Ahti and Hepburn 1967), which reflect generally less accumulation of peat and more influence of mineral soil water (Jeglum 1972). The complexity of vegetation within the wetlands was evident through a discrepancy in stand numbers between the sedge fen and shrub fen; 12 and 10 stands for the shrub fen and sedge fen respectively, with the subjective classification, compared to 19 and three stands with the objective classification.

In the first instance, the two communities were broadly defined on the basis of physiognomy, where 25% cover of shrubs distinguished "shrub carr" (shrub fen) from open "meadow" (grass-sedge fen) (White 1965). However, the more subtle differences and similarities between the shrub fen and grass-sedge fen were apparent when herbaceous vegetation was used as a basis for classification.

The variability of wetland vegetation is due largely to an environmental-complex gradient. Jeglum (1972) reported moisture and nutrients to be more important than disturbance (wave action) in influencing wetlands in the Mixedwood Section of the Boreal Forest in Saskatchewan. Similarly, Walker and Coupland (1968) found that the distribution of herbaceous species in Saskatchewan sloughs was strongly affected by water regime and somewhat less by salinity, while soil data showed very little association with species distribution.

The floristic composition of the shrub fen and sedge fen communities compared favorably to other studies of wetland vegetation in the Mixedwood Section (Lewis and Dowding 1926; Lewis et al. 1928; Moss 1955; Moss and Turner 1961; Jeglum 1972). Species particularly characteristic of these communities were *Carex* spp., *Calamagrostis* spp. and

Salix spp.

Figure 9 illustrates the relationship of vegetation to topography and soils. Grassland occurs on the uppermost slopes where solar radiation is greatest and drainage is rapid. Forest vegetation occupies mid-slope position, atop well to moderately-well drained soils. Shrub fen and grass-sedge fen communities occupy lower slope positions above poorly drained soils. This complex pattern of vegetation, topography and soils is a reflection of drainage, and the underlying parent material or glacial drift (Lang 1974). Consequently, a diverse habitat exists throughout the study area.

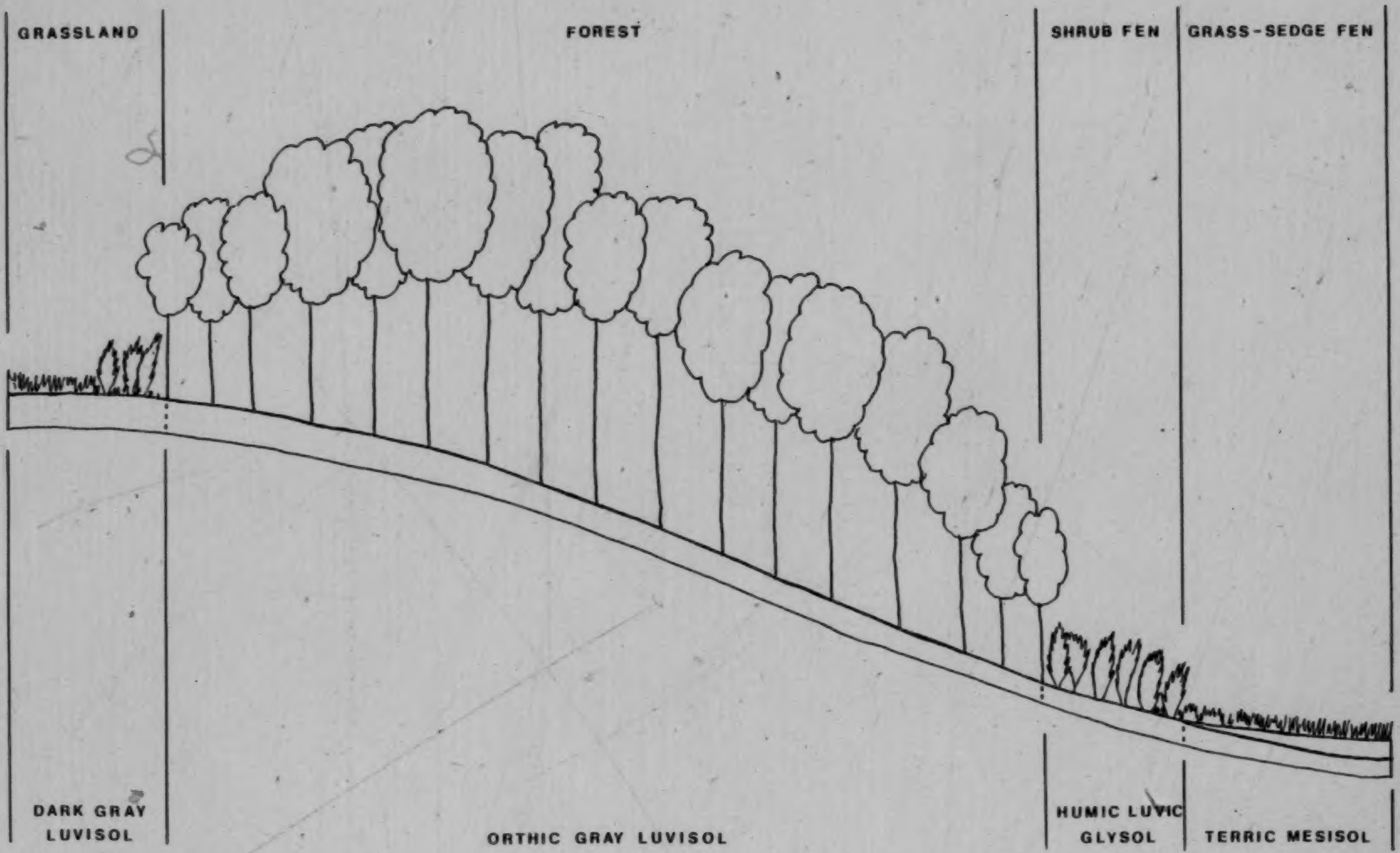

Figure 9. Diagrammatic sketch of the four plant communities and their relationship to four major soils along a soil catena.

V. Production and Utilization

A. Results

Browse

Neither CAG yield nor use of browse differed significantly by year (Table 5). However, there was a slight upward trend in yield the second year (1978) in both the forest and shrub fen communities. There was a similar upward trend in browse use in the forest community, but a downward trend in the shrub fen from 1977 to 1978. Percent use, relative to CAG, was slightly lower in both communities the second year.

Both yield and subsequent use also differed by community type as influenced by species composition and productivity (Table 5). The shrub fen had about eight times as much CAG biomass as did the forest community. However, the forest community is approximately four times greater in area than the shrub fen which would balance yield and use between these two communities. Percentage use, relative to CAG of browse, was essentially equal for both communities and served as an index of browsing pressure. Current annual growth, and also part of the two and three-year-old wood was consumed.

In the forest community 70% of annual biomass yield and more than 75% of total use was of *Corylus cornuta* (Table 6). The remaining biomass that was produced and consumed was relatively evenly divided among five other species. Of

Table 5. Yield (kg/ha) and use of available browse in the forest (n = 10) and shrub fen (n = 12) communities.

Community	1977					1978				
	Yield		Use			Yield		Use		
	Mean	±2SE	Mean	±2SE	%	Mean	±2SE	Mean	±2SE	%
Forest	7	± 2	17	± 7	243	10	± 4	19	± 8	190
Shrub Fen	64	±49	154	±134	241	66	±47	127	±68	192
Total	71	±51	171	±141	241	76	±51	146	±76	192

Note: Yield refers to current annual growth.

Table 6. Yield (kg/ha) and use of available browse by species in the forest community (n = 10).

Species	1977					1978				
	Yield		Use			Yield		Use		
	Mean	±2SE	Mean	±2SE	%	Mean	±2SE	Mean	±2SE	%
Corylus cornuta	5	±3	13	±7	269	7	±4	15	±8	202
Amelanchier alnifolia	1	±+	2	±+	195	2	±1	3	±2	183
Populus tremuloides	+[a]	±+	1	±+	374	+	±+	1	±+	299
Populus balsamifera	+	±+	+	±+	103	+	±+	+	±+	74
Salix bebbiana	+	±+	+	±+	47	+	±+	+	±+	18
Salix discolor	+	±+								
Total	7	±2	17	±7	259	10	±4	19	±8	198

[a] Less than 1.

these, only *Amelanchier alnifolia* and *Populus tremuloides* had biomass yield or use equal to or greater than 1 kg/ha.

Consumption relative to CAG also differed by year and species (Table 6). Use over all species was about 24% lower in 1978 than in 1977. *Populus tremuloides* appeared to be most heavily utilized in 1977, followed by *Corylus cornuta* which was five times more productive. Consumption of *Populus balsamifera* was 50% less than *Amelanchier alnifolia* but 50% greater than *Salix bebbiana*.

Salix spp. accounted for approximately 95% of the yield and corresponding use of biomass in the shrub fen community (Table 7). *Salix discolor*, which was somewhat more productive, and *Salix planifolia*, contributed more than 50% to overall biomass yield in both years. When *Salix pyrifolia* is included, the three species contributed 85% of overall use in 1977. But in 1978, 75% of overall use was attributed to *Salix planifolia* and *Salix pyrifolia*. Most of the remaining total annual biomass that was yielded and consumed was divided fairly evenly among four other species. Nearly equal to one another but much less productive were *Betula papyrifera* and *Populus balsamifera*, which were also more productive than *Populus tremuloides* and *Amelanchier alnifolia*.

Consumption of browse in the shrub fen, as in the forest, varied by year and species (Table 7). Overall consumption in 1978 decreased by 20% from that in 1977. *Salix planifolia*, *S. pyrifolia*, and *Populus tremuloides* were

Table 7. Yield (kg/ha) and use of available browse by species in the shrub fen community (n = 12).

Species	1977					1978				
	Yield		Use			Yield		Use		
	Mean	±2SE	Mean	±2SE	%	Mean	±2SE	Mean	±2SE	%
Salix discolor	22	±26	26	±38	117	20	±30	7	± 9	35
Salix planifolia	15	±17	86	±89	560	17	±12	76	±54	451
Salix petiolaris	7	± 7	4	± 4	60	5	± 4	4	± 3	75
Salix maccalliana	6	± 6	10	±11	169	6	± 7	8	± 9	123
Salix bebbiana	6	± 5	3	± 3	50	4	± 4	4	± 4	86
Salix pyrifolia	5	± 5	19	±17	374	8	± 7	19	±16	226
Betula papyrifera	2	± 2	3	± 3	162	2	± 3	4	± 6	193
Populus balsamifera	1	± 2	2	± 4	159	2	± 4	2	± 4	103
Populus tremuloides	+[a]	± +	1	± 2	284	+	± +	3	± 5	363
Amelanchier alnifolia	+	± +	+	± +	118	+	± +	+	± +	58
Total	64	±49	154	±134	239	66	±47	127	±68	192

[a] Less than 1.

most heavily utilized during both years. *Salix bebbiana and S. petiolaris* were utilized least in 1977, whereas *S. discolor* and *Amelanchier alnifolia* were utilized least in 1978.

Herbaceous Forage

Grassland

Annual yield of herbaceous and woody forage in the grassland varied by year and community (Table 8). Above-ground biomass was markedly greater in 1977 as compared to 1978. Of the two grassland phases, shrubby grassland was slightly more productive than grassland. Herbaceous biomass was evenly divided between grasses and forbs (Table 9). Grass yield differed significantly among grassland phases but forb yield did not. There was a consistent trend in both years for forbs to be more productive in the shrubby grassland.

Similarly, browse[14] differed among phases and forage classes in the grassland (Table 9). Twigs and leaves contributed substantially to overall forage yield in the shrubby grassland but not in the grassland phase. Litter also appeared to differ relative to year and phase.

The grassland community appeared to be grazed both summer and winter, as noted by the difference in biomass between caged and uncaged plots. Less forage was available in uncaged plots in both phases during the summer of 1978

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[14] Includes mostly *Rosa acicularis* and *Symphoricarpos occidentalis* which happened to be present in the plot; browse was not measured per se, in the grassland.

Table 8. Annual yield (kg/ha) and use of herbaceous forage and browse after summer grazing in the grassland community (n = 24).

Phase	1977						1978					
	Caged		Uncaged		Use		Caged		Uncaged		Use	
	Mean	±2SE	Mean	±2SE	Mean	%	Mean	±2SE	Mean	±2SE	Mean	%
Grassland (n = 12)	2789	±356	2538	±426	251	9	3211	±491	1907	±327**	1304	41
Shrubby Grassland (n = 12)	3010	±322	3191	±287	0	0	3299	±528	2584	±402**	715	22
Total (n = 24)	2900[a]	±239	2864	±313	36	1	3255[b]	±353	2245	±290**	1010	31

** Significantly less than caged according to the paired t-test ($P < 0.01$).

a, b Include approximately 4% and 6% woody browse by weight, respectively.

Table 9. Annual yield (kg/ha) of herbaceous forage and browse in the grassland community (n = 24).

Forage class	1977				1978			
	Grassland		Shrubby Grassland		Grassland		Shrubby Grassland	
	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE
Grass	1331	±266	890*	±180	1453	±307	742**	±176
Forb	1333	±303	1380	±298	1500	±393	1854	±571
Twig[a]	37	± 34	202**	± 82	112	± 90	268	± 80
Leaf[b]	88	± 82	539	±206	146	±110	435	±123
Litter	1254	±396	1049	±185	568	±190	991	±283

* Significant difference in biomass between phases, according to the paired t-test (* $P < 0.05$; ** $P < 0.01$).

[a,b] Refer to browse.

(Table 8); and except for the shrubby grassland in 1979, during both spring seasons (Table 10).

Use during the summer of 1978 was much greater than in 1977 (Table 8). Grasses, forbs and to a lesser extent litter, were all grazed the second summer in the grassland community (Table 11), and its two phases (Table 12). Consumption of forbs was almost twice that of grasses, while browse consumption was similar to that of grasses. Use was greater in the grassland phase than in the shrubby grassland.

Overall utilization during spring 1978 was somewhat greater than in 1979 (Table 10). But, whereas the grassland phase appeared to be more heavily grazed during the second spring season, the shrubby grassland was very heavily grazed during the spring of 1978, but lightly grazed the following spring.

Grass-Sedge Fen

Annual yield of herbaceous wetland forage was approximately 20% greater in 1978 than in 1977 (Table 13). This was primarily a consequence of an increase in precipitation.

Dead plant material from previous years' growth was much less than annual biomass production (Table 13). As with annual yield, *Carex* spp. accounted for more litter than *Calamagrostis canadensis*, especially in 1978 when this amount was significantly greater.

Table 10. Residual herbaceous forage (kg/ha) and browse in spring in the grassland community (n = 24).

Phase	1978						1979					
	Caged		Uncaged		Use		Caged		Uncaged		Use	
	Mean	±2SE	Mean	±2SE	Mean	%	Mean	±2SE	Mean	±2SE	Mean	%
Grassland (n = 12)	1534	±221	896^{**}	±321	638	42	1528	±340	717^{**}	±406	811	53
Shrubby Grassland (n = 12)	2104	±291	1510^{**}	±240	594	28	1818	±243	1744	±393	74	4
Total (n = 24)	1819	±250	1203^{**}	±234	616	34	1673	±213	1230^{**}	±350	443	26

** Significantly less than caged according to the paired t-test ($P < 0.01$).

Table 11. Annual yield (kg/ha) and use of herbaceous forage and browse after summer grazing in the grassland community (n = 24).

Forage class	1977						1978					
	Caged		Uncaged		Use		Caged		Uncaged		Use	
	Mean	±2SE	Mean	±2SE	Mean	%	Mean	±2SE	Mean	±2SE	Mean	%
Grass	1110	±182	1151	±228	0	0	1098	±228	857**	±166	241	22
Forb	1356	±208	1254	±225	102	8	1677	±347	1003**	±270	674	40
Twig	120	± 56	126	± 53	0	0	190	± 67	144	± 55	46	24
Leaf	313	±143	333	±135	0	0	291	±101	242	±103	49	17
Litter	1151	±218	1058	±178	93	8	780	±189	673*	±162	107	14

* Significantly less than caged according to the paired t-test (* $P < 0.05$; ** $P < 0.01$)

Table 12. Annual yield (kg/ha) and use of herbaceous forage and browse after summer grazing in two phases of the grassland community (n = 24).

Forage class	Grassland (n = 12)						Shrubby Grassland (n = 12)					
	Caged		Uncaged		Use		Caged		Uncaged		Use	
	Mean	±2SE	Mean	±2SE	Mean	%	Mean	±2SE	Mean	±2SE	Mean	%
1977												
Grass	1331	±266	1284	±422	47	4	890	±180	1018	±164	0	0
Forb	1333	±303	1150	±322	183	14	1380	±298	1358	±316	22	2
Twig[a]	37	± 34	30	± 24	7	19	202	± 82	223	± 67	0	0
Leaf[a]	88	± 82	74	± 67	14	16	539	±206	592	±150	0	0
Litter	1254	±396	890	±212	364	29	1049	±185	1226	±259	0	0
1978												
Grass	1453	±307	1035**	±264	418	29	742	±176	678	±152	64	9
Forb	1500	±393	771**	±248	729	49	1854	±571	1234	±451	620	33
Twig	112	± 90	37	± 30	75	67	268	± 80	251	± 57	17	6
Leaf	146	±110	64	± 50	82	56	435	±123	419	±138	16	4
Litter	568	±190	507	±182	61	11	991	±283	839	±237	152	15

* Significantly less than caged according to the paired t-test (* $P < 0.05$; ** $P < 0.01$).

[a] Refers to browse.

Table 13. Annual yield (kg/ha) and litter of *Carex* spp. and *Calamagrostis canadensis* in the grass-sedge fen community (n = 25).

Species	Annual Yield				Litter			
	1977		1978		1977		1978	
	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE
Carex spp.[a]	3721	±455	4316	±477	1667	±601	1576	±444
Calamagrostis canadensis	3067	±541	4124**	±672	1357	±356	1071	±327
Average	3394	±365	4220**	±421	1512	±432	1324	±333

[a] Mostly *Carex atherodes*.

** Significantly greater than 1977 according to the paired t-test ($P < 0.01$).

B. Discussion

Browse

Annual yield of browse in the forest and shrub fen was consistently less than consumption largely because of differences in twig diameter-weight relationships of current annual growth (Appendix I), and number of browsed twigs (Appendices J and K). Mean twig diameter and therefore corresponding weight of unbrowsed twigs, as well as twig number, were less than for browsed twigs. Since consumption of CAG cannot exceed 100%, old growth (and/or twigs larger in diameter than that for CAG twigs), must have been browsed also, to account for greater diameter-weight of browsed vs unbrowsed twigs. This is not unexpected since Telfer (1976) also reported more than 100% use for some highly palatable browse species in parts of EINP not nearly as heavily stocked as the study area. If continued, such excessive use may eventually lead to "browsing out" of many shrubs, since few species are tolerant of more than 60 to 75% removal of CAG during fall and winter before being destroyed (Julander 1937; Young and Payne 1948; Aldous 1952; Garrison 1953b; Penner 1978). Conversely, these researchers indicated that light to moderate browsing pressure tended to favour greater browse yield.

Natural succession would be affected by prolonged heavy use. A range trend study conducted in various exclosures and elsewhere throughout EINP, showed that moderate to heavy browsing impeded succession of *Populus tremuloides* and retarded normal growth of shrubs, though stem density remained unaffected (Milner 1977). In a similar assessment of browsing conditions in The Park (Bouckhout 1971), browsing significantly retarded sapling growth of *Populus tremuloides*, *P. balsamifera*, and *Betula papyrifera* which in turn retarded succession to forest. Growth of other browse species was impeded but not seriously depleted.

The shrub fen was much more productive than the forest because of the predominance of *Salix* spp. Its growth form, that of a multiple-stemmed vs a single-stemmed shrub, resulted in greater total stem density and therefore more annual twigs (Appendices J and K). Also, average diameter-weight per twig was much larger for *Salix* spp. in the shrub fen than for either *Corylus cornuta* or *Amelanchier alnifolia* in the forest community (Appendix I).

Differences in stem density, frequency, twig number and diameter-weight also accounted for variable yield of species within and between communities. The presence or absence of particular species was the most important determinant that influenced species yield between communities (Appendix L). It explained the wide difference in yield for some species that occurred in both forest and shrub fen.

Despite consumption exceeding 100% of annual growth, a substantial portion of annual growth for most species remained unbrowsed and therefore still available (Appendices J and K). In addition, consumption varied markedly among species (Tables 6 and 7). These observations may partially reflect food selection and preference of the ungulates in question.

Although these results bear some similarity to those of Telfer (1976), they differ markedly because of differences in methodology, stocking rate and location. For instance, aspen and balsam poplar together contributed approximately 64% of total browse yield north of Highway 16 (Telfer 1976) but only a negligible amount in this study. In this as opposed to the former study, methodology did not allow for adequate sampling of "edge" where the two poplar species were most abundant. Also, the stocking rate of elk and moose in the study area, (10.5 animals km^2 in 1977; 8.7 animals km^2 in 1978), was greater than that of The Park in general, particularly in 1977. This may explain the extremely heavy utilization in the study area, as compared to the moderate to heavy use over the remainder of The Park. The lighter stocking rate in 1978 also accounted for less browse utilization that year, compared to 1977 (Table 6).

Herbaceous Forage

Grassland

Herbaceous forage yield was substantially greater than that reported by Telfer (1972) and Milner (1977) for upland meadows north of Highway 16. This difference became still greater when annual twigs and leaves, which were more prevalent in the shrubby grassland than in the grassland phase, were included with herbaceous forage. Late placement of exclosure cones in 1977, thereby allowing for an extended grazing period, as well as less precipitation that year probably accounted for seemingly less yield than in 1978.

The grassland was lightly to moderately grazed during the winter, and especially during the summer of 1978. This was somewhat less than, but comparable to, the winter grazing received by a portion of The Park north of Highway 16 (McGillis 1968). Whereas both 1978 and 1979 seasons of winter and spring grazing were relatively comparable, a large discrepancy existed between summer grazing seasons. The difference in time of cage placement, long after leaf flush in late spring of 1977, compared to before leaf flush in the spring of 1978, partly accounted for this difference. This was probably further compounded through preference by elk and deer for the first green shoots of grass in spring (Holsworth 1960; Cairns 1976).

Use was greater in the grassland phase than in the shrubby grassland phase because of the barrier effect of shrubs (Bailey 1970), and the preponderance of more palatable species, especially grasses. Trampling, as well as replacement of some cages that became uprooted through animal activity, also contributed to the difference in use between the two phases. Utilization may have been less than actually observed due to the influence of cages on microclimate. Owensby (1969) reported forage production under cages in True Prairie vegetation to be 717 kg/ha greater than in uncaged areas in ungrazed pastures. Apparent differences in percentage consumption among species and forage classes may have suggested forage preference (Stoddart et al. 1975).

Grass-Sedge Fen

Annual yield in the sedge fen community corresponded favourably with that of similar communities described for The Park (Telfer 1972) and elsewhere (Corns and Schraa 1962; Corns 1974; Penner 1978; Reynolds et al. 1978). The slight difference in yield between the two major species may have been due to differing growth habit requirements and individual species characteristics.

Productivity of herbaceous wetland vegetation is closely tied to water regime, particularly duration, extent and depth of water during spring run-off (Jeglum 1972). Water level may be altered by precipitation and thereby affect herbage yield. This may explain partly the increase in productivity in 1978 over 1977 since precipitation was greater the second year (Table 1).

Utilization of the sedge fen was not assessed since bison, the prime foraging ungulate of this community type, was excluded from the exclosure. Holsworth (1960), Cairns (1976) and Telfer and Cairns (1979), reported that in The Park, sedge fen vegetation formed a major portion of the diet of bison during the winter season. Similar findings were reported for bison during all seasons in the Northwest Territories (Reynolds 1978). These studies clearly indicate the significance of the grass-sedge fen as a source of forage for bison.

VI. Chemical Composition

A. Results

Crude Protein

Crude protein differed markedly among forage types (Table 14). Browse leaves contained the greatest amount of crude protein of both woody and herbaceous forage types; more than double that of twigs. Upland grasses contained crude protein in amounts similar to twigs but less than the other three herbaceous species.

Significant variation in crude protein was observed among leaves and twigs of woody species (Table 15). The highest crude protein was in *Salix pyrifolia*. Among twigs, *Corylus cornuta* and *Amelanchier alnifolia* contained the least amount of crude protein.

Crude protein did not differ between summer and winter twigs (Table 14). Some species, particularly *Salix* spp. decreased in crude protein while *Corylus cornuta* and *Amelanchier alnifolia* increased in crude protein during the same period.

Phosphorus

Phosphorus varied considerably among woody and herbaceous forage types (Table 14). Woody leaves contained the highest percentage of phosphorus. Twigs and upland grasses contained the least phosphorus.

Phosphorus levels differed widely among species of browse leaves and corresponding twigs (Table 15).

Table 14. Chemical composition (%) of some woody and herbaceous forages (n = 4).

Forage Class	Protein		Phosphorus		Calcium		C : P	Ash		ADF		ADL		ADL : ADF
	Mean	±2SE	Mean	±2SE	Mean	±2SE		Mean	±2SE	Mean	±2SE	Mean	±2SE	
Woody														
Leaves	16.9	±1.6	0.35	±0.04	1.28	±0.19	3.7	6.2	±0.5	24.3	±2.2	10.2	±1.6	0.42
Twigs - summer	8.0	±0.8	0.21	±0.03	0.77	±0.09	3.7	3.7	±0.3	51.1	±1.6	21.6	±1.7	0.42
Twigs - winter	7.7	±0.5	$\overset{***}{0.16}$	±0.01	0.76	±0.09	4.8	$\overset{**}{3.1}$	±0.3	$\overset{***}{37.8}$	±1.4	$\overset{***}{14.8}$	±1.0	0.39
Herbaceous														
Grass[a]	8.2a[c]	±1.5	0.20a	±0.03	0.46a	±0.05	2.3	7.0b	±0.5	39.0b	±1.1	3.9ab	±0.2	0.10
Calamagrostis canadensis	13.3b	±1.3	0.24ab	±0.02	0.43a	±0.08	1.8	5.2a	±0.6	39.3b	±2.2	5.0b	±1.0	0.13
Carex spp.[b]	11.9b	±0.9	0.25ab	±0.02	0.62b	±0.09	2.5	6.9b	±1.3	34.1a	±2.7	3.3a	±0.8	0.10
Forb	11.8b	±1.6	0.30b	±0.06	1.40	±0.13	4.5	8.9c	±0.3	32.2a	±2.4	7.0c	±0.7	0.22

[a] Mostly *Poa pratensis*, *Agropyron subsecundum* and upland *Carex* spp.

[b] Mostly *Carex atherodes*, *C. aquatilis* and *C. rostrata*.

[c] Means followed by the same letter in each column do not differ significantly according to the Student-Newman-Keuls multiple range test, ($P < 0.05$).

[*] Significant difference between seasons according to the F-test (** $P < 0.01$; *** $P < 0.001$).

Table 15. Percent crude protein, phosphorus and calcium in current annual growth of 9 browse species (n = 4).

Species	Crude Protein						Phosphorus						Calcium					
	Summer				Winter		Summer				Winter		Summer				Winter	
	Leaves		Twigs		Twigs		Leaves		Twigs		Twigs		Leaves		Twigs		Twigs	
	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE
Salix maccalliana	16.8bcd[a]	±1.3	8.5ab	±0.8	8.0b	±0.3	0.29d	±0.02	0.21c	±0.01	0.14c***	±0.01	1.30ab	±2.10	0.73cd	±0.07	0.72bc	±0.09
S. petiolaris	17.3bcd	±1.7	8.9a	±0.6	8.1b	±0.9	0.32d	±0.04	0.25c	±0.03	0.16abc***	±0.02	1.10bc	±0.19	0.78bcd	±0.08	0.50d**	±0.07
S. planifolia	18.1abc	±3.0	9.2a	±0.9	8.4b	±0.8	0.31d	±0.01	0.23c	±0.02	0.15c***	±0.01	0.83cd	±0.15	0.59de	±0.03	0.72bc	±0.16
S. pyrifolia	20.9a	±1.9	9.0a	±1.0	8.0b	±0.5	0.30d	±0.06	0.24c	±0.06	0.15bc*	±0.02	0.74d	±0.08	0.57de	±0.03	0.56cd	±0.05
Populus tremuloides	15.0cd	±1.3	7.1bc	±0.3	7.4bc	±0.3	0.34d	±0.03	0.20c	±0.01	0.18a*	±0.00	1.52a	±0.25	0.84bc	±0.11	0.84b	±0.11
Betula papyrifera	19.3ab	±2.6	8.9a	±1.4	8.5b	±0.7	0.42c	±0.08	0.24c	±0.04	0.18ab*	±0.01	1.10bc	±0.05	0.43e	±0.06	0.42d	±0.05
Corylus cornuta	15.1cd	±0.9	5.6d	±0.5	6.2d	±0.3	0.34d	±0.05	0.13d	±0.00	0.11d**	±0.01	1.60a	±0.29	1.10a	±0.08	1.20a	±0.09
Populus balsamifera	13.8d	±0.4	8.5ab	±1.0	7.8b	±0.4	0.32d	±0.03	0.22c	±0.04	0.17abc	±0.02	1.70a	±0.24	0.95ab	±0.21	0.80bc	±0.12
Amelanchier alnifolia	16.4bcd	±0.8	6.7cd	±0.2	6.9cd	±0.1	0.50b	±0.04	0.22c	±0.06	0.18ab	±0.01	1.60a	±0.21	0.99ab	±0.17	1.00b	±0.09

[a] Means followed by same letter in each column do not differ significantly according to the Student-Newman-Keuls multiple range test ($P < 0.05$).

* Significant difference between summer and winter twigs according to the unpaired t-test (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Amelanchier alnifolia and *Betula papyrifera* which contained the greatest amounts of phosphorus, differed from one another and from the remaining species. *Corylus cornuta* twigs contained the least phosphorus. Phosphorus content was more variable in winter twigs than in summer twigs.

Twig phosphorus content declined from summer to winter for all species but *Populus balsamifera* and *Amelanchier alnifolia*.

Calcium

Calcium differed widely among forage types (Table 14). Forbs and woody leaves had the greatest amounts of calcium. Twigs contained moderate amounts of calcium, substantially more than grasses and slightly more than sedges.

Calcium varied widely among species of browse leaves and twigs (Table 15). *Salix pyrifolia* and *S. planifolia* contained least calcium among leaves. Calcium content of summer twigs did not differ among *Salix* spp. but differed among other species. *Corylus cornuta* twigs contained the greatest amount of calcium during both seasons.

Calcium either increased, decreased or remained unchanged from summer to winter for twig species (Table 15). However these differences were significant only for *Salix petiolaris*.

Calcium:Phosphorus

Calcium to phosphorus ratios varied considerably among forage classes (Table 14) and browse species (Table 16). Especially high ratios among forage classes were observed

Table 16. Calcium : phosphorus ratio and percent ash in current annual growth of 9 browse species.

Species (n = 4)	C : P			Ash					
	Summer		Winter	Summer				Winter	
	Leaves	Twigs	Twigs	Leaves		Twigs		Twigs	
				Mean	±2SE	Mean	±2SE	Mean	±2SE
Salix maccalliana	4.3	3.5	5.1	5.9c[a]	±0.4	3.5cd	±0.4	2.9c*	±0.2
S. petiolaris	3.5	3.1	3.1	5.0cd	±0.5	3.6cd	±0.3	2.3cd**	±0.3
S. planifolia	2.6	2.6	4.8	5.2cd	±0.3	3.4cd	±0.4	2.8c	±0.4
S. pyrifolia	2.5	2.4	3.7	4.7d	±0.4	3.3cd	±0.4	2.5cd*	±0.1
Populus tremuloides	4.5	4.2	4.7	6.7b	±0.8	3.8bc	±0.3	3.5b	±0.3
Betula papyrifera	2.7	1.8	2.3	5.4cd	±0.6	2.9d	±0.4	2.0d**	±0.2
Corylus cornuta	4.8	8.3	11.1	7.0b	±0.8	4.3ab	±0.2	4.7a	±0.3
Populus balsamifera	5.2	4.3	5.1	7.8a	±0.3	4.8a	±0.4	3.7b**	±0.4
Amelanchier alnifolia	3.3	4.5	5.7	8.3a	±0.3	3.9bc	±0.2	3.9b	±0.3

[a] Means followed by the same letter in each column do not differ significantly according to the Student-Newman-Keuls multiple range test ($P < 0.05$).

* Significant difference between summer and winter twigs according to the unpaired t-test (* $P < 0.05$; ** $P < 0.01$).

for winter twigs and forbs. Ratios were relatively high for most leaf and twig species, particularly for twigs of *Corylus cornuta*.

Ash

Ash differed considerably among forage classes (Table 14). Forbs contained the greatest amount of ash; significantly more than other herbaceous types and more than woody types. Twigs contained the least amount of ash with comparable but greater amounts contained in sedges, upland grasses and leaves.

Ash differed widely among species of browse leaves and corresponding twigs (Table 16). *Populus balsamifera* and *Amelanchier alnifolia* contained the greatest amount of ash within leaves of browse species. Except for *Betula papyrifera, Corylus cornuta* and *Populus balsamifera*, no difference in ash existed among species of summer twigs. The ash content of winter twigs of *Salix* spp. differed from that of other species. *Corylus cornuta* contained the greatest amount of ash.

Ash varied significantly between summer and winter seasons for most twig species (Table 16). Five species decreased in ash content, whereas *Corylus cornuta* exhibited an upward trend in ash.

Acid-Detergent Fibre

ADF was quite comparable among woody and herbaceous forage classes except for summer twigs and leaves which represented the greatest and least amounts of ADF.

respectively (Table 14). Sedges and forbs had less ADF than grasses, marsh reed grass and winter twigs.

ADF varied among species of browse leaves and twigs (Table 17). ADF content of browse leaves was lowest for *Betula papyrifera* and highest for *Populus balsamifera*. ADF content of summer twigs was lowest for *Corylus cornuta*, and highest for *Salix pyrifolia*. ADF among winter twigs was highest and lowest for *Populus balsamifera* and *Amelanchier alnifolia*, respectively.

The decrease in ADF from summer to winter was highly significant for most twig species (Table 17). Only *Corylus cornuta* increased whereas two other species remained unchanged.

Acid-Detergent Lignin

ADL differed greatly among woody and herbaceous forage types (Table 14). ADL was much greater among woody as compared to herbaceous forage classes, particularly summer twigs, which contained the greatest ADL. Forbs contained the greatest amount of ADL among herbaceous forage.

ADL varied among leaves of browse species and twigs (Table 17). Leaves of four species contained the least of ADL. *Corylus cornuta* contained the least ADL, whereas *Salix* spp. exhibited the most ADL for summer twigs. ADL of winter twigs varied less than that of summer twigs. *Betula papyrifera* contained the most ADL.

ADL differed between summer and winter twig species (Table 17). All species decreased in ADL from summer to

Table 17. Percent ADF, ADL and ADL : ADF ratio in current annual growth of 9 browse species (n = 4).

Species	ADF						ADL						ADL : ADF		
	Summer				Winter		Summer				Winter		Summer		Winter
	Leaves		Twigs		Twigs		Leaves		Twigs		Twigs		Leaves	Twigs	Twigs
	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE			
Salix maccalliana	28.6ab[a]	±4.2	56.5c	±1.6	34.1d**	±2.5	14.3ab	±3.3	27.5b	±3.0	12.6c***	±0.6	.50	.49	.37
S. petiolaris	27.5abc	±4.3	58.4bc	±0.2	39.0b***	±1.4	15.4a	±3.0	29.2b	±1.6	13.5c***	±1.0	.56	.50	.35
S. planifolia	19.5de	±1.8	60.9ab	±2.1	35.2cd***	±2.9	7.3c	±1.1	29.6a	±2.3	14.2c***	±1.8	.37	.44	.40
S. pyrifolia	23.8bcd	±1.1	62.4a	±2.0	40.0b***	±1.2	11.6d	±0.6	29.0a	±1.9	13.9c***	±1.0	.49	.46	.35
Populus tremuloides	26.6abc	±3.6	49.9d	±1.0	37.5bc***	±0.9	11.2b	±2.4	22.9b	±1.2	14.7c***	±0.7	.42	.46	.39
Betula papyrifera	17.2e	±0.8	38.8e	±3.5	40.0b	±0.3	7.1c	±1.0	12.2c	±2.1	20.0a**	±1.3	.41	.31	.50
Corylus cornuta	23.2bcd	±0.5	35.4f	±1.0	37.5bc*	±0.8	5.4c	±0.3	8.2d	±0.6	14.6c***	±0.4	.23	.23	.39
Populus balsamifera	29.4a	±3.2	50.0d	±1.9	80.4e***	±1.6	12.5ab	±2.1 ±	23.3b	±2.3	12.8c***	±0.8	.42	.47	.42
Amelanchier alnifolia	22.6cd	±0.7	47.2d	±1.0	46.3a	±0.8	7.45c	±0.7	12.5c	±0.6	16.9b**	±1.2	.33	.27	.36

[a] Means followed by the same letter are not significantly different according to the Student-Newman-Keuls multiple range test ($P < 0.05$).

* Significant difference between summer and winter twigs according to the unpaired t-test (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

winter except *Betula papyrifera*, *Corylus cornuta* and *Amelanchier alnifolia* which increased.

Acid-Detergent Lignin:Acid-Detergent Fibre

The ratio of ADL:ADF varied markedly between and within species of leaves and twigs (Table 17). Leaves of *Corylus cornuta* contained the smallest proportion of ADL:ADF, less than 25%, while three of four willow species contained the highest ratios. Similarly, *Corylus cornuta* and to a lesser extent *Amelanchier alnifolia*, exhibited the smallest ADL:ADF ratios among summer twigs. This ratio was similar for winter twigs except for *Betula papyrifera* which possessed the highest ratio.

B. Discussion

Forage quality may be evaluated by an assessment of the nutrient components contained within a plant. One of the most important nutrient constituents is crude protein (% nitrogen X 6.25) which represents protein and non-protein nitrogen (Dietz 1970). Protein provides the amino acids used by rumen micro-organisms to effectively digest carbohydrates and fats (Dietz 1970).

Carbohydrates provide the chief source of energy in forage (Oldemeyer 1974). Readily digestible carbohydrates include sugars and starches which are contained within the cell. Less readily digestible, or structural carbohydrates, are contained within the cell wall and include cellulose, hemicellulose and undigestible lignin (Dietz 1970). The determination of ADF permits the calculation of hemicellulose (cell walls minus ADF) and cellulose (ADF minus lignin) (Van Soest and Moore 1965). Hemicellulose is of greater benefit to ruminants than cellulose, while lignin is undigestible.

Ash indicates the mineral composition of a plant (Kubota et al. 1970; Kubota 1974). However, the presence of silica may result in a misleading interpretation of actual mineral composition. Phosphorus is the most important mineral and is vital in many body processes, especially in the production of muscle energy through the action of adenosine triphosphate (ATP) (Dietz 1970). Calcium is the second most vital mineral. It is important in skeletal development, and as a component of blood. Winter forage usually contains adequate levels of calcium, but often contains marginal or inadequate levels of phosphorus (Dietz 1970). A wide Ca:P ratio adversely affects phosphorus metabolism. Therefore, a Ca:P ratio of 1:2 to 2:1 is recommended for cattle. However, a ratio of 7:1 may be acceptable if sufficient vitamin D is present (Maynard and Loosli 1969).

Crude Protein

There was considerable variation in crude protein among forage classes. Of particular note was the relatively high and low crude protein content of browse leaves and grass respectively, and the relatively low content of twigs. Kramer and Kozlowski (1960) reported that leaves and meristematic tissue contain most of the nitrogen content in trees and shrubs. This would explain the high concentration of crude protein in leaves compared to twigs. Similar results were borne out by Aldous (1945), Short and Harrell (1969), (Dietz 1972) and Penner (1978).

Grass was comparatively low in crude protein because it was collected in mid-summer while in an advanced stage of maturity. Nutritional studies of range forage in southern Alberta, alpine areas and elsewhere, have shown that by mid-summer, crude protein levels in grasses have been reduced by 50-75% (Johnston et al. 1962; Smoliak and Bezeau 1967; Johnston et al. 1968). Values of crude protein for sedge and marsh reed grass were similar to those obtained by others (Corns and Schraa 1962; Corns 1974). Forbs were reasonably high in crude protein since they generally maintain comparatively high nutritive content well into late summer (Dietz 1972).

Species and seasonal differences in crude protein were observed for leaves and twigs of browse. Such species variation has been influenced by factors such as soil moisture (Tew 1970), overstory (Halls and Epp 1969; Laycock and Price 1970), succession (Cowan et al. 1950), elevation (Deitz 1972), vegetation type and site (Cook and Harris 1950a), and soil (Hundley 1959). Crude protein of twigs did not change appreciably from summer to winter, comparable to results reported by Penner (1978), Deitz et al. (1958) and others.

Crude protein requirement for the maintenance of elk and moose has not been confirmed but has been documented for other ruminants. Values of 5.8 - 9.0% have been suggested as adequate for the maintenance of white-tailed deer (Bissell and Strong 1955; French et al. 1956; Dietz 1972; Holter et al. 1979). Greater levels of crude protein, in the order of 13-16%, have been reported as necessary for growth and reproduction (French et al. 1956; Murphy and Coates 1966). NAS-NRC (1976) recommends a minimum of 5.9% crude protein as necessary for beef cattle on a maintenance diet. Assuming that similar amounts of crude protein are required by elk and moose for maintenance, all forage classes and species provide an adequate amount of this nutrient.

Carbohydrates

The variability of ADF among forage classes and browse species was reasonably consistent with that reported by other researchers. Highest levels of ADF were found in twigs, grasses and sedges while moderate and low levels were observed in forbs and browse leaves, respectively. These were due largely to differences in stem:leaf ratios among forage classes. Fibrous carbohydrates are usually much more concentrated in stems than in leaves (Cook and Harris 1950a; Dietz 1972). Season of growth probably influenced these differences too, especially between forbs and grasses, since some forbs mature later in the growing season and thereby contain less fibre.

The level of ADF among browse species varied in like manner with that in other studies (Cowan et al. 1950; Gastler et al. 1951; Dietz 1972; Penner 1978). The decrease in ADF from summer to winter for *Salix* spp. is consistent with Penner (1978) but contradicts somewhat, the generally held belief that ADF increases with seasonal progression, particularly during the winter period. Dietz et al. (1958) and Dietz (1972) reported that five of seven, and four of five deciduous browse species respectively, increased in ADF from spring through winter, albeit some increases were very slight, especially from late summer-early fall through the dormant period. Gastler et al. (1951) also, reported increases in ADF from summer to winter for aspen, hazel, birch and saskatoon. The apparent wide difference in summer levels of ADF among the four species of *Salix* and the other five browse species appears to be inconsistent. A seasonal difference of this magnitude was not observed in Penner's (1978) work.

Lignin, a complex, relatively indigestible portion of cellulose that increases with seasonal progression, has been found to be inversely correlated with the digestibility of cellulose and hemicellulose (Kamstra et al. 1958; Short et al. 1974). Therefore, ADL and ADL:ADF ratios among grasses and domestic forages partially indicate their comparative digestibility. Among woody species, ADL and ADL:ADF ratios were not correlated with digestibility (Oldemeyer et al. 1977). Among forage classes the digestibility of herbaceous species is markedly greater than that of browse (Short et al. 1974). Because leaves contain only one half as much ADF as twigs, they receive a much greater forage quality rating. Among woody browse, CAG contains lower levels of lignin than old wood and therefore is relatively more digestible (Penner 1978; Short et al. 1972; Van Soest 1964). Woody forage wood be less digestible therefore, because old wood, as well as CAG, was consumed.

Minerals

Calcium, phosphorus and ash differed in relation to forage class and species. Herbaceous forage, particularly browse leaves and forbs, contained the greater amount of these three minerals than did grasses and twigs, similar to results reported by Cook (1972), Dietz (1972), and Short et al. (1972). These differences were probably a consequence of plant part and stage of maturity, two factors that influence nutritive values (Clarke and Tisdale 1945; Johnston et al. 1962; Short et al. 1972). The variability of calcium, phosphorus and ash among browse species was in accord with results of similar species reported by Cowan et al. (1950), Gastler et al. (1951), Cook (1972) and Penner (1978). Variation of these minerals may be attributable to a combination of site and vegetation factors (op cit.).

Studies have suggested the minimum requirement of phosphorus to be approximately 0.25% (French et al. 1955) and 0.16% (NAS-NRC 1976) for white-tailed deer, and cattle and sheep respectively. Ideally the Ca:P ratio should lie somewhere between 1:2 and 2:1 although a ratio of 7:1 may be acceptable if sufficient vitamin D is present (Maynard and Loosli 1969). However, Dietz et al. (1972) concluded that where ratios were greater than 5:1, calcium interferred with phosphorus metabolism. Assuming that similar levels apply to elk and moose, it would appear that all forage classes and most browse species furnish marginal calcium and phosphorus within acceptable ratios.

Although herbaceous forage contains a sufficient amount of calcium and phosphorus, phosphorus may be deficient during the critical winter period (Dietz 1972). At the same time, the increase in calcium results in a wider, and therefore less desirable Ca:P ratio.

Ample calcium, adequate phosphorus and acceptable Ca:P ratios were apparent in leaves and twigs of most browse species. Leaves contained adequate phophorus but the relatively high Ca:P ratio for most species may offset this. Although *Corylus cornuta* was the sole twig species deficient in phosphorus during summer, several species appeared to be phosphorus deficient during winter, coupled with unacceptably high Ca:P ratios. Phosphorus of these and other deciduous browse species has been reported to be deficient during the dormant season (Dietz 1972; Penner 1978). However, effects of these deficiencies may be counteracted by utilization of other species which provide adequate levels of these nutrients (Cook 1972).

It could not be determined if ash contained an adequate amount of minerals since silica often makes up a large proportion of ash (Morrison 1957).

Although it appeared that the forage contained a sufficient quantity of nutrients to meet maintenance requirements, less than these amounts may have actually been available due to the consumption of two and three-year-old wood. Nutrients such as crude protein, phosphorus, and calcium are present in lesser amounts in old wood, whereas greater amounts of ADF and ADL are present in old wood (Short et al. 1972; Short et al. 1974; Penner 1978).

VII. Discussion

A. Resource Utilization

Habitat Preference

Insufficient data precluded a statistical determination of habitat preference. However, some insight into habitat preference may be gained through inspection of these data and results reported by Provo (1980).

The forest, shrub fen and grassland communities were used extensively, based upon forage use within each community (Table 18). The grass-sedge fen received little use although this observation cannot be positively confirmed since forage use data were not collected in this community. The forest and shrub fen communities were equally preferred, as judged by the similarity of percent forage use relative to yield in both communities.

The apparent equal preference shown toward the forest and shrub fen communities was the result of a heavy stocking rate, and a mixed ungulate population. Heavy stocking rate limits free choice of forage, resulting in diet expansion and ultimately habitat selection (Ellis et al. 1975). Specific forage preferences of elk and moose are complementary and therefore promote use of all habitats. Provo (1980) suggested that elk selected for the forest community, whereas moose selected for the shrub fen community when these two ungulate species were placed together. Preference by moose for shrubby communities,

Table 18. Total yield and use (kg) of forage, 1977-78.

Community	Area		Year	Yield				Use					
				Herbage		Browse		Herbage				Browse	
								Summer		Winter			
	ha	%		kg/ha	kg	kg/ha	kg	kg/ha	kg	kg/ha	kg	kg/ha	kg
Forest (n = 10)	415[a]	69	1977 1978			7 10	2906 4152					17 19	7058 7889
Grass-Sedge Fen (n = 25)	97	16	1977 1978	3394 4220	330,236 410,606								
Shrub-Feb (n = 12)	59	10	1977 1978			64 66	3782 3901					154 127	9101 7506
Grassland (n = 12)	28	5	1977 1978	2900[b] 3255[c]	80,910 90,814			36[d] 1010	1004 28,179	616 443	17,186 12,360		
Total	599	100	1977	6294	411,146	71	6688	36	1004	616	17,186	171	16,159
			1978	7475	501,420	76	8053	1010	28,179	443	12,360	146	15,395

Note: Area does not include water (120 ha or 17% of total study area).
Use of browse applies to fall-winter period.

[a] Does not include 3 ha of white spruce forest.

[b,c] Include approximately 4% and 6% respectively, woody browse by weight.

[d] Extremely low due to cage placement in late spring, after grazing initiation.

particularly those containing willows, has also been reported by others (Holsworth 1960; Berg and Phillips 1974; Cairns 1976; Telfer 1978; and Penner 1978). Rounds (1981) reported elk preference for grassland, shrubland, and recent burns, and rejection of mixed forest of quaking aspen-white spruce, white spruce, jack pine (*Pinus banksiana*) and bog communities. Moose showed preference for immature aspen forest and rejection of shrubland, white spruce and bog communities.

The grassland community was utilized during both summer and winter seasons (Table 18). Use was attributed mainly to elk. Food habits and habitat studies of elk indicate their preference for herbaceous forage, especially grasses and sedges (Holsworth 1960; Knight 1970; Cairns 1976; Hunt 1977; Telfer and Cairns 1979). The grassy and shrubby phases of the grassland were not equally preferred according to a comparison of their relative forage use. The grassy phase was preferred due to its relatively greater abundance of grass, and the barrier effect of shrubs (Bailey 1970).

Very minimal use was observed in the grass-sedge fen, since neither moose nor elk exhibit much preference toward this community, except perhaps in early spring (Holsworth 1960; Cairns 1976). However, Telfer and Cairns (1979) reported elk summer diets consisted of 95% herbage, 71% being sedge. The extensive use of all communities except the grass-sedge fen, indicated the importance of habitat diversity.

Forage Preference

Forage preference was measured for 10 species of browse in the shrub fen, based upon the ratio of percent of total yield to percent of total use of forage. Ratios greater than 1 indicated species preference, whereas ratios less than 1 indicated species avoidence (Table 19). Chi square and the Bonferroni *z* statistic (Neu et al. 1974) indicated *Salix planifolia* to be the only species that was significantly preferred. Several species were significantly avoided, or were neither preferred nor avoided.

The relative preference or avoidance among species and between years is illustrated in Figure 10. Preference and avoidance generally remained stable from year to year. However *Salix bebbiana* and *Betula papyrifera* exhibited less yearly stability than the other species.

The variable preference portrayed among the 10 browse species was a result of some facet of palatability: characteristics or conditions of a plant which stimulate a selective (or avoidance) response by animals (Heady 1964). These include physical characteristics such as morphology, vigor, availability, and chemical characteristics such as nutrient composition.

Species preference was related to absolute weight, frequency and chemical composition. No relationship was evident between absolute weight and preference, as judged by inspection, but a positive relationship did exist between frequency and preference. This may explain partially the

Table 19. Preference (+), avoidance (-) or indifference (0) for species of browse in the shrub fen community.

Species	Preference-Avoidance Indices			
	1977		1978	
Salix bebbiana	.21	-	.45	0
S. discolor	.49	-[a]	.18	-
S. maccalliana	.71	0	.64	0
S. petiolaris	.00	-	.39	-
S. planifolia	2.35	+[b]	2.36	+
S. pyrifolia	1.57	0	1.18	0
Populus tremuloides	1.20	0	1.90	0
Betula papyrifera	.68	-	1.01	0
Populus balsamifera	.66	-	.53	-
Amelanchier alnifolia	.50	0	.50	0

a, b avoidance (-) or preference (+) according to chi square test ($P < 0.05$).

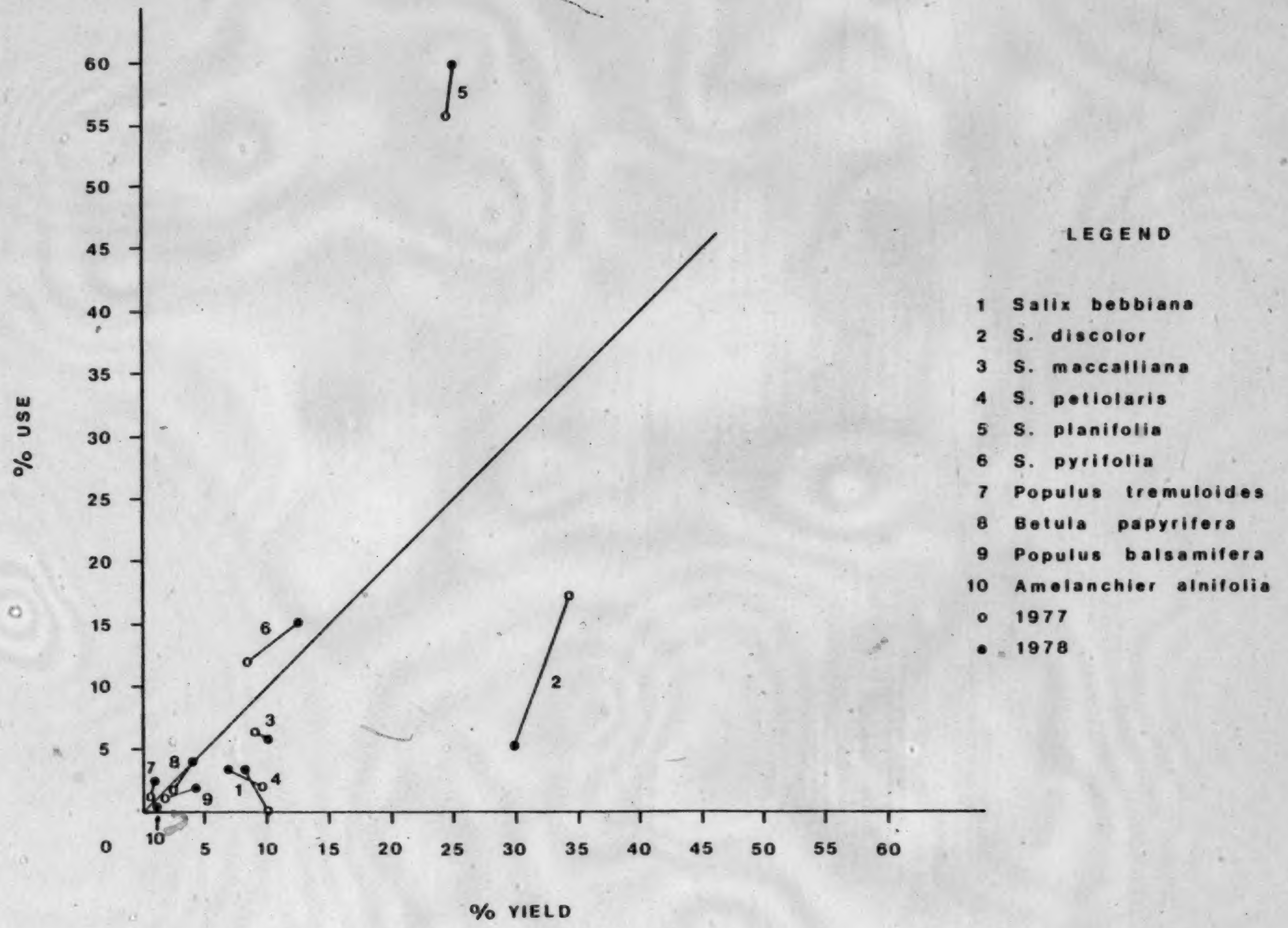

Figure 10. Preference (above diagonal) and avoidance (below diagonal) of 10 species of browse in the shrub fen plant community during 1977 and 1978.

preference for *Salix planifolia*, which exhibited the greatest frequency of all species (Appendix L). Nystrom (1980) also, reported feeding moose calves generally sample shrubs in proportion to their availability, ultimately consuming more browse from stems of preferred species and less from others.

Quality or chemical composition of a plant, especially protein, has been found to be correlated with palatability and ultimately with preference (Dietz and Yeager 1959; Dietz 1972; and Lindlof et al. 1974). However, no correlation was found between protein and preference. Nor was there a correlation between overall chemical composition, and preference or avoidance, according to Hotelling's T-squared or the F-statistic. These observations appear to be similar to those noted by Penner (1978) who concluded that no relationship existed between the chemical content of willows and their preference by moose. However, Penner (op cit.) did report lower ADL:ADF ratios in browsed twigs as opposed to unbrowsed twigs. Arnold and Hill (1972), in a review of findings related to chemical factors in plants and animal selection, concluded that no relationship exists between chemical composition of a plant and the preference animals show for it.

Neither chemical composition nor availability were solely responsible for the apparent preference exhibited for some browse species. Other additional palatability factors likely influenced preference. Penner (1978) concluded that moose repeatedly selected willow plants that had been previously browsed, regardless of species, but left untouched those plants which had not been previously browsed. Penner (op cit.) attributed this apparent preference for browsed plants to the excessive quantity of new, succulent shoot growth in comparison to that of unbrowsed plants. Longhurst et al. (1968) found that taste played a significant role in the palatability of certain browse species by deer. Tannins and coumarins have been associated with negative selection. Depth of snow has also been found to influence selection of forage (Telfer 1978). These and other combinations of factors such as associated species, previous knowledge and physiology, probably influenced selection (Heady 1964).

B. Carrying Capacity

Carrying capacity of the study area may be discussed by a consideration of daily forage intake, particularly as applied to the browse resource. Browse is the major type of forage in the diet of moose (Peek 1974), and is often its sole source of forage during winter. Browse is generally supplemental to herbaceous forage in the diet of elk (Hunt 1977). Browse becomes increasingly important as herbaceous forage becomes limited, or is rendered otherwise unavailable because of snow cover.

Hypothetical estimates of daily forage intake are presented in Table 20. These estimates were based upon a

Table 20. Estimated daily forage intake by moose and elk.

Year	Species	Number of animals		Animal Use Days	Total Forage Use		Daily Forage Intake
		Total	No/km^2		Browse (kg)	Herbage (kg)	(kg/animal)
1977-78	Moose	34	5.7	6868	16,159		2.4
	Elk	29	4.8	5858		17,186	2.9
	Total	63	10.5	12,726			
1978-79	Moose	16	2.7	3232	15,395		4.8
	Elk	36	6.0	7272		12,360	1.7
	Total	52	8.7	10,504			

Note: Animal Use Days - number of animals × 202 days of forage use (October 1 - April 20).

number of assumptions and were derived in the following manner: browse consumption attributed to moose was assumed to be from leaf drop to leaf flush, or from approximately October 1st to April 20th; a foraging period of 202 days. This foraging period, multiplied by the number of animals of each species for each of two years, represented the number of animal use days. The total use of browse or herbage, divided by the number of animal use days for each species, resulted in an estimate of daily forage intake/head/day.

The hypothetical estimate of daily forage intake by moose during the 1977-78 fall-winter foraging period, was similar to that reported by Gasaway and Coady (1974), and Crete and Bedard (1975), approximately 2.5 kg/head/day. This estimate was probably considerably less than calculated due to browse utilization by elk. The estimated daily forage intake of herbage by elk appears to approximate that suggested by other researchers (Thorne and Butler 1976; Robbins et al. 1981). Holsworth (1960) reported as much as 30% browse in the rumen of elk slaughtered during December in EINP. Daily forage intake for both species actually may be higher than calculated due to consumption of browse from broken stems which were not accounted for.

During the 1978-79 foraging period, estimated daily forage intake of moose doubled, while overall browse consumption decreased by approximately five percent from the previous year. In actuality, this marked change in estimated daily forage intake was due to a drastic decline in the moose population. As in the previous year, elk would be expected to again supplement their diet with browse. If such supplementation were in the ratio of 50% browse, 50% herbage, not unrealistic for elk winter diets (Hobbs et al. 1981), both species would still realize a net increase in daily forage intake over the previous year.

Theoretical estimates of daily forage intake for both species in 1978-79, adjusted for browse consumption by elk, appear to approach more closely, typical daily voluntary intakes; approximately two percent of body weight (Thorne and Butler 1976). This value is generally lower during winter, since animals require less energy due to decreased activity (Knorre 1959). The reduced moose population resulted in a more favorable daily forage intake rate for both species. However, these levels of daily forage intake may still be insufficient in meeting requirements for maintenance. The substantial amount of second and third year growth which was presumably consumed, is much less digestible than CAG (Penner 1978). Also, daily forage intake decreases with a decrease in digestibility of forage (Robbins and Moen 1975).

The initial stocking rate within the study area of 10.5 animals per km² was probably in excess of carrying capacity. However, as stocking rate declined, it probably began to approach carrying capacity and progressive stabilization of habitat. Rounds (1977) suggested that fluctuations in the moose and elk population of Riding Mountain National Park, Manitoba, eventually became coincident through habitat stabilization. Telfer and Scotter (1975) suggested that 4.4 moose and 4.4 elk, or 8.8 animals per km^2 was a feasible stocking rate for these species in EINP. Except for the proportion of moose to elk, this corresponds to the overall stocking rate within the study area for 1978-79. The apparent heavy browsing throughout the duration of the study, even at the lower stocking rate, suggests a stocking rate in excess of carrying capacity. A stocking rate of less than 8.7 animals per km^2 would be more in line with carrying capacity of the area.

A stocking rate in excess of carrying capacity dramatically affects animal behavior and vegetation. Blair and Brunett (1980) reported that an increased use of low choice or non-preferred species by deer, suggested excessive pressure was being exerted on the decreasing supply of more preferred browse. They concluded that this signalled an overpopulation of deer in relation to their food supply. In an assessment of food selection by North American deer and their response to over-utilization of preferred plant species, Klein (1970) concluded that when food becomes limited, either through ecological change or increases in population density, the preferred plant species of highest forage quality are reduced and often eliminated by the deer.

The apparent heavy browsing as a consequence of heavy stocking rate, if sustained, may result in the eventual elimination of some species. The relatively different levels of browsing intensity tolerated by species would undoubtedly compound this situation. The apparent scarcity in the study area and throughout The Park in general (Telfer 1976) of highly preferred species such as red osier dogwood, chokecherry and cranberry, may be a result of past heavy browsing, coupled with the variable resistance of these species to browsing. A further indication of the effects of past heavy browsing was exemplified by severe hedging, low stature and a general lack of vigor observed for many plants, especially of saskatoon and willow species. Where these species were protected from browsing, plants appeared to be robust and vigorous.

C. Management Implications and Recommendations

The results of the study indicated various relationships between the range and its ungulate population. Forest, shrub fen and grassland communities were utilized extensively, whereas the grass-sedge fen was utilized rarely, if at all. Forest and shrub fen were especially favoured because of their relatively high browse productivity. Very heavy use of browse was evident due to the large population of moose and elk. CAG as well as two and three-year-old wood was consumed. Consumption of old wood, in addition to CAG, provided additional bulk for rumen fill. Despite this, however, poor digestibility of old wood may leave animals nutritionally deficient, particularly in energy and protein.

Gradual deterioration of range, and the consumption of browse that is poorly digested, are two of the major problems which result from overstocked range. The following recommendations are suggested to minimize these problems:

1. Decrease and maintain stocking rate to more closely approximate the carrying capacity of the range; perhaps three moose and three elk per km^2; less elk if bison are to be included in the animal population.

2. Prescribed burning or other method of brush manipulation to increase grass production in the grassland.

3. Clear small portions of the forest to increase habitat diversity, and the growth and availability of nutritious browse.

4. Periodically monitor forage yield, use and range condition, and restock accordingly.

VIII. Summary and Conclusions

A study was conducted in EINP, Alberta, during 1977-1979 in an enclosed, 723 ha area that contained an initial population of 34 moose and 29 elk, and a final population of 16 moose and 34 elk. The purpose of the study was to collect data relative to the production and chemical composition of forage, and to its use by the ungulate population.

Four major communities were recognized by means of a physiognomic classification of vegetation: forest (*Populus-Aralia*) community (415 ha), grass-sedge fen (*Calamagrostis-Carex*) community (97 ha), shrub fen (*Salix-Calamagrostis*) community (59 ha), and grassland (*Poa-Symphoricarpos*) community (28 ha). A principle components analysis of species and stands indicated that the most important environmental gradients determining floristics were moisture and light intensity. A cluster analysis of stands indicated their degree of association, and thereby provided an objective means of community classification and selection. Each community was described by its species composition as related to canopy cover and frequency of herbaceous species; and frequency and density of woody species.

Average annual growth of browse produced within a 0.5-2.5 m height range was 8 and 65 kg/ha in the forest and shrub fen, respectively. Average browse utilized within the same height range was 18 and 140 kg/ha in the forest and shrub fen, respectively. *Corylus cornuta* and *Amelanchier* *alnifolia* contributed most to browse production in the forest community, whereas *Salix* spp., particularly *Salix planifolia*, *S. pyrifolia* and *S. discolor*, contributed most to browse yield in the shrub fen. The difference between yield and use of browse indicates that two and three-year-old wood, in addition to CAG, was consumed. Such heavy utilization, if prolonged, may eventually lead to "browsing out" of some species, and an alteration in plant succession.

The grassland community was grazed extensively during summer and winter, as evidenced by significant differences between the weight of caged and uncaged forage. The average yield and use of forage after summer grazing (1978) was 3255 and 1010 kg/ha, respectively or 31% use. This compares to an average winter use of 30% for 1978 and 1979. The marked difference in percentage use between the grassland and shrubby grassland phases during summer and winter grazing periods, indicated a preference toward the former community relative to the latter. Preference for the grassland phase was due to its greater yield of grass than the shrubby grassland, 1392 versus 816 kg/ha, respectively; and the barrier effect of shrubs in the latter phase.

Yield of annual herbaceous forage in the grass-sedge fen averaged 3807 kg/ha and was significantly greater the second year. Greater precipitation during the spring period of 1978 may have accounted for greater forage yield than in 1977. Yield of *Carex* spp. averaged 4018 kg/ha, whereas

Calamagrostis canadensis averaged 3596 kg/ha.

Chemical composition of annual herbaceous forage and browse collected in summer, and summer and winter, respectively, was determined by an analysis of crude protein, calcium, phosphorus, ash, ADF and ADL. Generally, each constituent varied significantly among forage class, species and season. Herbaceous species contained greater amounts of crude protein, phosphorus, calcium and ash than woody species. Conversly, woody species contained greater amounts of ADF and ADL than did herbaceous forage. Phosphorus, ADF and ADL in woody twigs decreased from late summer through winter. *Salix* spp. in particular, showed a consistent trend in the decline of all nutrients during the dormant period. In general, the chemical composition of forage was adequate to meet requirements of animals on a maintenance diet. Ca:P ratios were within acceptable levels except for summer and winter twigs of *Corylus cornuta* which contained exceptionally high ratios.

Habitat preference by elk and moose could not be determined statistically because of insufficient data. However, it did not appear that any one habitat was preferred since utilization was evident in all communities except the grass-sedge fen.

Forage preference and avoidance of 10 browse species was evident. Preference was thought to be related to forage availability, as well as to other factors. No relationship was evident between forage preference and chemical composition.

Hypothetical estimates of daily forage intake suggested the range was at or near carrying capacity before introduction of the elk population. Upon introduction of elk, carrying capacity was exceeded but was gradually being restored as the moose population declined, and the habitat became more stable. Although estimated daily forage intake appeared reasonable, it was probably insufficient to meet maintenance requirements due to the decreased digestibility of two and three-year-old wood that was consumed.

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Appendices

Appendix A. Twig diameter-weight relationships.

Standardized twig diameter-weight relationships were determined in the following manner: 50 CAG twigs ≤2.5 cm in length were collected over the range of basal diameters as browsed by the animals. Each twig was marked and its basal diameter measured to the nearest 1/100 cm using a vernier caliper. Twigs of each species were separately placed in paper bags and allowed to air-dry for several days at room temperature, after which their basal diameters were again measured. The bags of twigs were then placed in a forced-air oven for 24 hours at 70°centigrade to drive off any remaining moisture. The oven-dry weight of the twigs was then determined. Correlation and linear regression of twig diameter- weight was used to define an equation to predict twig weight from twig diameter for each important browse species.

Appendix B. Basal area (m^{-2} ha), DBH (cm) and height (cm) of aspen in the forest community, (n = 10).

Stand	Diameter (cm)									
	1.5-3.5	3.5-5.5	5.5-7.5	7.5-9.5	9.5-11.5	11.5-13.5	13.5-15.5	$\overline{X}$	DBH	Height
110	2.3	16.0	6.9	2.3				6.9	19.5	23.3
136		6.9	23.0	6.9	4.6			10.4	18.3	18.7
148		6.9	32.1	9.2	2.3			12.6	16.7	19.7
152		2.3	2.3	6.9				3.8	17.7	15.9
155		4.6	25.2	9.2				13.0	15.0	17.8
159		2.3	9.2	6.9			2.3	5.2	17.3	16.6
170		2.3	11.5	6.9	2.3			5.7	17.3	18.5
179		6.9	21.0	6.9		2.3	4.6	8.3	16.8	19.3
206		11.5	23.0	6.9				13.8	16.2	17.7
228			11.5	6.9				9.2	18.3	17.6
Total	2.3	59.7	165.7	69.0	9.2	2.3	6.9	88.9	173.1	185.0
$\overline{X}$	0.2	6.0	16.6	6.9	0.9	0.2	0.7	8.9	17.3	18.5

Appendix C. Prominence index of important species in the forest community (n = 10).

Species	Stands									
	110	159	170	179	155	148	136	206	152	228
Woody										
Rubus strigosus	5	4	8	4				8		1
Viburnum edule	5	3	2			1		5		
Symphoricarpos occidentalis		1		6		2			4	10
Amelanchier alnifolia	2		1	2				2	7	
Rosa acicularis[a]	3		1	8					4	4
Lonicera dioica	1	2		1						2
Corylus cornuta	2					1				
Prunus virginiana	5									
Herbaceous										
Aralia nudicaulis	21	23	17		76	42	39	35	14	20
Calamagrostis canadensis	6	8	27	25	1	4	5		9	4
Maianthemum canadense	8	4	17	4	11	2	4	11	3	9
Lathyrus ochroleucus	36	4	7	12	3	5	6	6	3	4
Rubus pubescens	16	30	9	10	8	20	6	5	5	
Mertensia paniculata		6	3	10	4	6	3	2	1	5
Fragaria virginiana	3	8	4	6		1	3		4	3
Galium boreale	3	4	2	10		1	2	1		4
Cornus canadensis	2	2	2		7	8	5	1		
Viola adunca								1		
Thalictrum venulosum	3		2							5
Aster ciliolatus				3				2		1
Epilobium angustifolium				4			1			3
Arnica cordifolia				2		1				2
Vicia americana	4	3	6	5	3				1	1
Petasites palmatus		4	2			2				1
Mentha arvense										1
Solidago spp.	4		8	8			3			1
Pyrola asarifolia			1	1			3		3	
Heracleum lanatum	2								3	
Equisetum arvense			7				2			
Lysimachia thyrsifolia			3							
Anemone canadensis			2							
Sanicula marilandica			1							
Lysmachia ciliata			1							
Disporum trachycarpum					2		1			
Carex spp.		3								
Aster conspicuous		1								
Urtica gracilis	1									

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[a] includes *Rosa woodsii*.

Appendix D. Prominence index of important species in the shrub fen community (n = 12).

Species	Stands											
	603	605	563	604	555	548	544	503	511	506	508	534
Woody												
Lonicera involucrata		1				10			5		3	3
Ribes spp.							5		7			
Rubus strigosus								2	1			
Ledum groenlandicum		1		5								
Herbaceous												
Calamagrostis canadensis	25	51	80	56	50	47	51	90	50	61	18	5
Carex atherodes	2	12	15	1			2			17	26	2
Carex rostrata	39				4		5					
Equisetum arvense		5			2	21	5		34		7	15
Scutellaria galericulata					2			12	4	2	11	16
Stellaria longifolia	1				13			3		1		1
Aster puniceus		1	3	2		1				11	7	
Mentha arvensis					4	2			1	12	5	1
Impatiens capensis	11					5	3				2	6
Galeopsis tetrahit						14	13	1		3		3
Galium trifidum		2			3			7				
Petasites sagittatus		1		4					5	1		3
Mertensia paniculata							1		3	2	3	
Carex aquatilis								4	5	2	2	
Caltha palustris	8			5	2							
Rubus pubescens		3				2						
Arennaria spp.	11				10							
Potentilla palustris		1	2						3			
Ramex occidentalis			1	12								
Stachys palustris						3						11
Cicuta douglasii		2										
Galium triflorum				2							1	
Urtica gracilis						2				2		
Fragaria virginiana				2								
Glyceria grandis								2				
Andromeda polifolia									2			
Polygonum amphibium										3		
Carex lasiocarpa											2	
Species "f"	9				17					6		
Species "g"				4	5							
Moss		3	2	4								

Appendix E. Prominence index of important species in the grass-sedge fen community (*n* = 10).

Species	Stands									
	351	330	318	353	336	342	306	307	435	401
Woody										
Populus balsamifera								7		
Ribes spp.					3					
Herbaceous										
Calamagrostis canadensis		2	43	91	88	92	98	81		72
Carex atherodes	38	85							98	59
Carex aquatilis	18		44							
Poa palustris	13	6	7			2	3			
Galium trifidum	10	5	1			2				
Scutellaria galericulata		3	9	1	2	2		3		
Equisetum arvense		6		1	9	2	8	2		
Epilobium glandulosum	1	4			1					1
Carex rostrata					5	8		8		
Carex lasiocarpa		4	2							
Galeopsis tetrahit						12	2			
Mentha arvensis				2						
Eleocharis palustris	4									
Lysimachia thyrsifolia	3									
Bidens cernua	2									
Rumex occidentalis			3							
Stellaria longifolia						6				
Arennaria spp.						1				
Stachys palustris								3		
Geum allepicum								1		

Appendix F. Prominence index of important species in the grassland community (n = 8).

Species	Stands							
	305	370	369	399	367	311	356	301
Woody								
Symphoricarpos occidentalis	22	24	18	8	17		4	35
Rosa acicularis	1	3	3		13	1	10	
Populus balsamifera			2	2			5	
Rubus strigosus							11	2
Amelanchier alnifolia		4	3					
Herbaceous								
Poa pratensis	63	11	55	26	45	25	47	51
Agropyron subsecundum	36	1	33	23	10	14		45
Bromus ciliatus	4	47	14	2	34	5	10	10
Galium boreale	2	10	35	36	8	7	27	10
Achillea millefolium	10	4	14	29	7	28	10	30
Solidago spp.	22	32	19	5	8	13		16
Vicia americana	2	3	4	4	1	5	4	22
Aster laevis		1	9		4		31	3
Anemone canadense	8	19	4		6	4		2
Fragaria virginiana	14				3	19	6	1
Thalictrum venulosum		5		11	4			6
Phleum pratense			2		1	7	1	
Agastache foeniculum			2	2	2			1
Trifolium repens						4	13	4
Calamagrostis canadensis		5		3	9			
Lathyrus ochroleucas		2				3	3	
Artemisia ludoviciana				20			13	
Calamagrostis neglecta					18		1	
Juncus balticus				11			5	
Carex spp.							6	2
Agrimonia striata	5					3		
Aster pansus			4	2				
Cirsium arvense	4		1					
Agropyron trachycaulum				4			1	
Species "h"							8	
Carex foenea				5				
Carex lasiocarpa							5	
Eleocharis palustris				4				
Viola spp.						3		
Potentilla gracilis				2				
Pyrola asarifolia						2		
Antennaria neglecta							2	
Species "i"							2	
Lathyrus venosus							1	
Campanula rotundifolia			1					
Sanicula marilandica							1	

Appendix G. Prominence index of important species in the shrub fen community (as determined by cluster-ordination) (n = 19).

Species	Stands																		
	503	435	605	401	563	555	603	548	307	534	306	506	604	353	511	342	508	336	554
Woody																			
Ledum groenlandicum			1										5						
Populus balsamifera									7										
Herbaceous																			
Calamagrostis canadensis	90		51	72	80	50	25	47	81	57	98	61	56	91	50	92	18	88	51
Carex atherodes		98	12	59	15		2			2		17	1				26		2
Carex rostrata						4	39			8						8		5	
Equisetum arvense			5			2		21	2	15	8			1	34	2	7	9	5
Scutellaria galericulata	12					2			3	16		2		1	4	2	11	2	
Mentha arvensis						4		2	10	1	5	12		2	1		5		
Petasites sagittatus			1							3	10	1	4		5			7	
Galeopsis tetrahit	1							14		3	2	3				12			
Aster puniceus			1		3			1		2		11	2				7		
Stellaria longifolia	3					13	1			1		1				6			
Impatiens capensis							11	5		6						2		3	
Potentilla palustris			1		2						3				3	2			
Carex aquatilis	4											2			5		2		
Mertensia paniculata												2			3		3		1
Galium trifidum	7		2			3										2			
Species "f"						17	9					6							
Arennaria spp.						10	11									1			
Stachys palustris								3	3	11									
Caltha palustris						2	8						5						
Rumex occidentalis					1					1			12						
Rubus pubescens			3					2											
Urtica gracilis								2				2							
Galium triflorum													2				1		
Polygonum amphibium												3							
Cicuta douglasii			2																
Andromeda polifolia															2				
Solidago spp.																		2	
Glyceria grandis	2																		
Lysimachia thyrsifolia										2									
Fragaria virginiana													2						
Carex lasiocarpa																	2		
Geum allepicum									1										

Appendix H. Prominence index of important species in the grass-sedge fen community (as determined by cluster-ordination) (n = 3).

Species	Stands		
	330	318	351
Potentilla palustris	7	7	13
Galium trifidum	5	1	10
Carex atherodes	85		38
Carex aquatilis		44	20
Calamagrostis canadensis	2	43	
Scutellaria galericulata	3	9	
Carex lasiocarpa	4	2	
Epilobium glandulosum	4		1
Moss spp.			7
Equisetum arvense	6		
Eleocharis palustris			4
Rumex occidentalis		3	
Lysimachia thyrsifolia			3
Bidens cernua	2		

Appendix I. Weighted mean diameter of current growth (DCG) (mm), diameter at point of browsing (DPB) (mm) and corresponding twig weights (g) of 11 browse species.

Species	1977				1978			
	DCG	wt.	DPB	wt.	DCG	wt.	DPB	wt.
Salix bebbiana	3.15	0.68	3.45	1.12	3.21	0.72	3.51	1.17
S. discolor	3.54	1.03	4.31	2.30	3.79	1.26	4.35	2.36
S. maccalliana	2.59	0.26	4.12	1.65	2.70	0.30	3.46	0.91
S. petiolaris	4.43	2.38	3.59	1.59	4.43	2.39	3.73	1.80
S. planifolia	2.02	0.16	3.69	1.30	2.35	0.26	3.81	1.43
S. pyrifolia	2.74	0.26	4.31	1.68	3.19	0.44	4.10	1.41
Corylus cornuta	1.77	0.07	2.55	0.38	2.05	0.12	2.50	0.36
Amelanchier alnifolia	1.64	0.08	2.26	0.27	1.91	0.12	2.25	0.26
Populus tremuloides	2.13	0.08	3.70	0.82	2.36	0.11	3.44	0.64
Populus balsamifera	3.67	0.41	4.26	0.98	4.51	0.79	4.52	1.18
Betula papyrifera	1.90	0.08	2.58	0.32	2.22	0.13	2.90	0.47

Appendix J . Number of annual twigs produced, browsed and unbrowsed for browse species in the forest community (n = 10).

Species	1977						1978					
	Produced		Browsed		Unbrowsed		Produced		Browsed		Unbrowsed	
	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE
Corylus cornuta	71,240	±40,378	34,953	±19,111	36,288	±22,057	63,695	±32,999	42,120	±22,495	21,575	±13,966
Amelanchier alnifolia	15,355	±10,041	8.699	± 5,422	6,656	± 5,075	14,654	± 8.652	12,441	± 7,428	2,213	± 1,634
Populus tremuloides	3,284	± 2,873	1,182	± 1,210	2,109	± 1,818	2,881	± 2,557	1,532	± 1,289	1,349	± 1,665
Populus balsamifora	235	± 469	101	± 202	134	± 267	172	± 344	85	± 170	87	± 174
Salix bebbiana	274	± 547	78	± 156	196	± 391	176	± 352	20	± 40	156	± 313
S. *discolor*	248	± 497			248	± 497						
Total	90,636	±54,805	45,013	±26,101	45,624	±30,105	81,578	±44,904	56,334	±31,422	25,380	±27,752

Appendix K. Number of annual twigs produced, browsed and unbrowsed for browse species in the shrub fen community (n = 12).

	1977						1978					
Species	Produced		Browsed		Unbrowsed		Produced		Browsed		Unbrowsed	
	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE	Mean	±2SE
Salix bebbiana	8,698	± 2,030	2,710	± 751	6,257	± 1,498	6,094	± 1,496	3,200	± 906	2,893	± 836
S. discolor	21,540	± 7,262	11,291	± 4,770	10,249	± 2,764	15,664	± 6,844	2,870	± 1,047	12,794	± 5,827
S. maccalliana	21,888	± 6,492	5,890	± 1,887	15,998	± 4,906	21,136	± 6,427	8,666	± 2,791	12,469	± 4,130
S. petiolaris	2,768	± 852	2,484	± 737	283	± 126	2,203	± 530	2,181	± 531	22	± 13
S. planifolia	94,259	±30,060	65,783	±19,660	28,476	±10,632	65,954	±13,926	53,357	±10,901	12,597	± 3,502
S. pyrifolia	19,990	± 5,174	11,518	± 2,998	8,472	± 2,515	18,965	± 4,876	13,283	± 3,354	5,682	± 1,601
Populus tremuloids	5,356	± 2,764	1,469	± 747	3,888	± 2,019	6,264	± 3,295	4,013	± 2,109	2,251	± 1,186
Betula papyrifera	21,773	± 6,684	6,008	± 2,417	13,184	± 4,105	17,112	± 5,920	9,349	± 3,460	7,763	± 2,503
Populus balsamifera	3,054	± 1,706	2,013	± 1,118	1,041	± 588	2,882	± 1,593	1,986	± 1,089	896	± 504
Amelanchier alnifolia	187	± 108	62	± 36	125	± 72	84	± 48	21	± 12	62	± 36
Corylus cornuta	157	± 91			157	± 91	194	± 112			194	± 112
Total	199,940	±63,223	109,228	±35,121	88,130	±29,316	156,552	±45,067	98,926	±26,200	57,623	±20,250

Appendix L . Number (ha^{-1}), relative density (%) and relative frequency (%) of stems (or clumps) of 11 browse species in the forest (n = 10) and shrub fen (n = 12) communities.

Species	Forest				Shrub Fen			
	Number		Density	Frequency	Number		Density	Frequency
	Mean	±2SE			Mean	±2SE		
Salix bebbiana	39	± 25	+[a]	2	655	± 128	4	8
S. discolor	101	± 44	1	2	2415	± 743	10	8
S. maccalliana					1869	± 523	10	11
S. petiolaris					532	± 130	4	5
S. planifolia					8198	±1375	45	30
S. pyrifolia					2013	± 468	22	11
Corylus cornuta	10433	±1916	60	48	6	± 4	+	+
Amerlanchier alnifolia	3537	± 631	23	28	42	± 24	+	+
Populus tremuloides	1309	± 296	14	18	1909	±1002	2	11
Betula papyrifera	45	± 28			1162	± 414	3	14
Populoides balsamifera	39	± 25	+	2	320	± 167	+	2
Total	15503	±2965			19121	±4978		

[a] Less than 1.

Appendix M. List of Species

TREES

Betula papyrifera	Paper Birch
Populus balsamifera	Balsam Poplar
Populus tremuloides	Aspen Poplar

SHRUBS

Amelanchier alnifolia	Saskatoon
Alnus crispa	Green Alder
Cornus stolonifera	Dogwood
Ledum groenlandicum	Labrador Tea
Linnaea borealis var. *americana*	Twin-flower
Lonicera dioica var. *glaucescens*	Twining Honeysuckle
Lonicera involucrata	Bracted Honeysuckle
Prunus virginiana	Chokecherry
Ribes lacustre	Bristly Black Current
Ribes oxyacanthoides	Wild Gooseberry
Ribes spp.	Current Species
Rosa acicularis [15]	Prickly Rose
Rubus strigosus	Wild Red Raspberry
Salix bebbiana	Beaked Willow
Salix discolor	Pussy Willow
Salix maccalliana	Willow
Salix petiolaris	Willow
Salix planifolia	Willow

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[15] Includes *Rosa woodsii*.

Salix pyrifolia	Balsam Willow
Symphoricarpos occidentalis	Buckbrush
Viburnum edule	Cranberry

HERBS

Forbs

Achillea millefolium	Common Yarrow
Achillea sibirica	Milfoil
Adoxa moschatellina	Moschatel
Agastache foeniculum	Giant Hyssop
Agrimonia striata	Agrimony
Anemone canadensis	Canada Anemone
Andromeda polifolia	Bog Rosemary
Antennaria neglecta	Pussy-toes
Apocynum androsaemifolium	Spreading Dogbane
Aralia nudicaulis	Wild Sarsaparilla
Arenaria lateriflora	Sandwort
Arenaria spp.	Sandwort Species
Arnica cordifolia	Arnica
Artemisia campestris	Wormwood
Artemisia ludoviciana	Prairie Sagewort
Aster ciliolatus	Lindley's Aster
Aster conspicuus	Showy Aster
Aster hesperius	Western Willow Aster
Aster laevis var. *geyeri*	Smooth Aster
Aster modestus	Aster
Aster pansus	Tufted White Prairie Aster

Aster puniceus	Purple-stemmed Aster
Aster spp.	Aster Species
Bidens cernua	Nodding Beggarticks
Campanula rotundifolia	Harebell
Caltha palustris	Marsh Marigold
Castilleja miniata	Indian Paintbrush
Chrysosplenium iowense	Golden Saxifrage
Cicuta douglasii	Water Hemlock
Circaea alpina	Enchanter's Nightshade
Cirsium arvense	Canada Thistle
Comandra pallida	Bastard Toad-flax
Cornus canadensis	Bunchberry
Disporum trachycarpum	Fairy-bells
Epilobium angustifolium	Fireweed
Epilobium glandulosum	Willow-herb
Equisetum arvense	Common Horsetail
Erigeron philadelphicus	Fleabane
Fragaria virginiana var. *glauca*	Wild Strawberry
Galeopsis tetrahit	Hemp Nettle
Galium boreale	Northern Bedstraw
Galium trifidum	Small Bedstraw
Galium triflorum	Sweet-scented Bedstraw
Geum allepicum var. *strictum*	Yellow Avens
Geum macrophyllum	Yellow Avens
Habenaria viridis	Bracted Orchid
Halenia deflexa	Spurred Gentian

Heracleum lanatum	Cow Parsnip
Hieracium canadense	Canadian Hawkweed
Impatiens capensis	Touch-me-not
Lactuca pulchella	Common Blue Lettuce
Lathyrus ochroleucus	Pea Vine
Lathyrus venosus	Purple Peavine
Lycopus uniflorus	Water Horehound
Lysimachia ciliata	Fringed Loosestrife
Lysimachia thyrsifolia	Tufted Loosestrife
Maianthemum canadense var. *interius*	Wild Lily-of-the-Valley
Mentha arvensis var. *villosa*	Wild Mint
Mertensia paniculata	Tall Mertensia
Mitella nuda	Mitrewort
Monarda fistulosa var. *menthaefolia*	Wild Bergamot
Moss spp.	Moss Species
Parnassia palustris var. *neogaea*	Grass-of-Parnassus
Petasites palmatus	Palmate-leaved Coltsfoot
Petasites sagittatus	Arrow-leaved Coltsfoot
Potentilla gracilis	Graceful Cinquefoil
Potentilla norvegica	Rough Cinquefoil
Potentilla palustris	Marsh Cinquefoil
Polygonum amphibium var. *stipulaceum*	Water Smartweed
Pyrola asarifolia	Common Pink Wintergreen
Ranunculus macounii	Macoun's Buttercup

Rorripa islandica	Yellow Cress
Rubus acaulis	Dwarf Raspberry
Rubus chamaemorus	Cloudberry
Rubus pubescens	Dewberry
Rumex occidentalis var. *fenestratus*	Western Dock
Sanicula marilandica	Snake-root
Scutellaria galericulata	Common Skullcap
Sium suave	Water Parsnip
Smilacina trifolia	Three-leaved Solomon's-seal
Solidago lepida	Goldenrod
Solidago spp.	Goldenrod Species
Stachys palustris var. *pilosa*	Hedge Nettle
Stellaria longifolia	Long-leaved Chickweed
Stellaria spp.	Chickweed
Sisyrinchium montanum	Blue-eyed Grass
Taraxacum officinale	Common Dandelion
Thalictrum venulosum	Veiny Meadow Rue
Trifolium repens	White Clover
Urtica gracilis	Common Nettle
Vicia americana	Wild Vetch
Viola adunca	Early Blue Violet
Viola rugulosa	Western Canada Violet
Viola spp.	Violet Species
	Grasses
Agropyron repens	Quack Grass
Agropyron subsecundum	Bearded Wheat Grass

Agropyron trachycaulum	Slender Wheat Grass
Bromus ciliatus	Fringed Brome
Calamagrostis canadensis	Marsh Reed Grass
Calamagrostis neglecta	Northern Reed Grass
Deschampsia caespitosa	Tufted Hair Grass
Elymus innovatus	Hairy Wild Rye
Glyceria grandis	Manna Grass
Koeleria cristata	June Grass
Phleum pratense	Timothy
Poa pratensis	Kentucky Bluegrass

Sedges and Rushes

Carex aquatilis	Water Sedge
Carex atherodes	Awned Sedge
Carex foenea	Sedge
Carex lasiocarpa	Sedge
Carex rostrata	Beaked Sedge
Carex spp.	Sedge Species
Eleocharis palustris	Spike Rush
Juncus balticus	Wire Rush

UNIDENTIFIED SPECIES

Species "C"
Species "D"
Species "E"
Species "F"
Species "G"
Species "H"
Species "I"
Species "J"